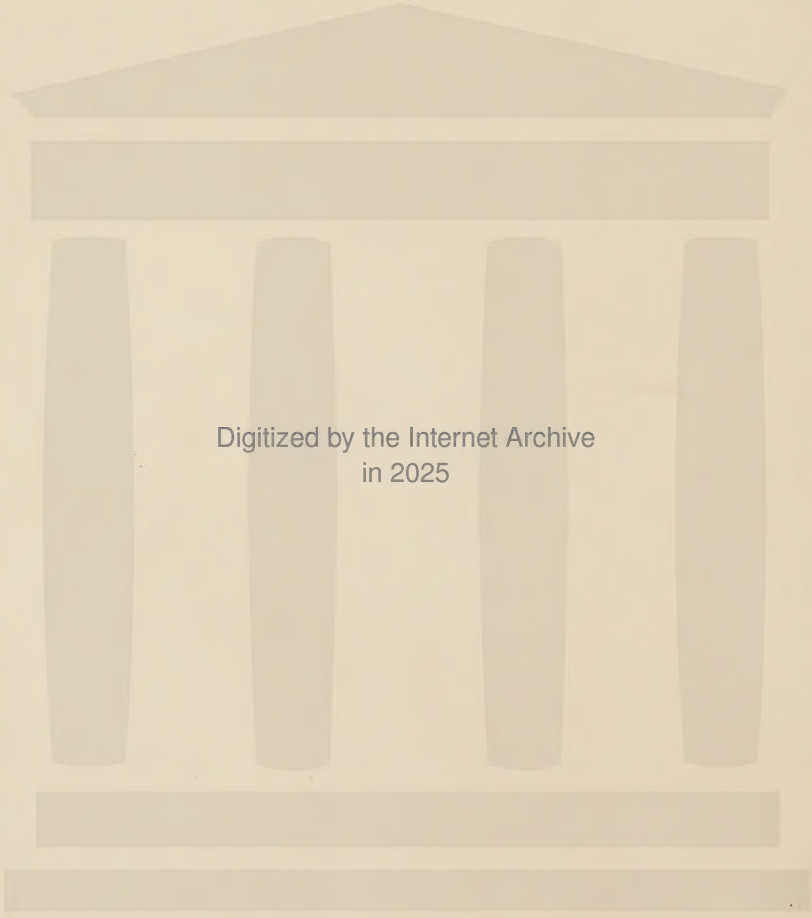
COMM. DEPT. AGRICULTURE
LIBRARY
S.N. 11448


Digitized by the Internet Archive
in 2025

https://archive.org/details/bulletin-of-entomological-research_1959-1960_50

BULLETIN

OF

ENTOMOLOGICAL RESEARCH.

ISSUED BY THE COMMONWEALTH
INSTITUTE OF ENTOMOLOGY

EDITOR: THE DIRECTOR

VOL. 50.

LONDON:

COMMONWEALTH INSTITUTE OF ENTOMOLOGY,
56, QUEEN'S GATE, S.W.7.

1960.

Commonwealth Agricultural Bureaux.

EXECUTIVE COUNCIL.

A. PERERA, *Chairman*, Ceylon.

C. K. REHEEM, *Vice-Chairman*, Pakistan.

W. G. ALEXANDER, C.B.E., United Kingdom.

J. G. MALLOCH, M.B.E., Ph.D., Canada.

E. J. DRAKE, Australia.

V. ARMSTRONG, Ph.D., New Zealand.

J. F. BROOKS, Union of South Africa.

S. KRISHNAMURTI, India.

W. W. K. VANDERPUYE, Ghana.

J. D. DE SILVA, Federation of Malaya.

J. E. C. COVENTRY, Federation of Rhodesia and Nyasaland.

C. E. LAMBERT, C.M.G., Colonial Territories.

Sir HERBERT HOWARD, *Secretary*, Farnham House, Farnham Royal, Nr. Slough, Bucks.

COMMONWEALTH INSTITUTE OF ENTOMOLOGY.

Director and Editor.
E. O. PEARSON, M.A.

Assistant Director.
R. G. FENNAH, M.A.

Assistant Editor.
W. RUTTLEDGE, M.A.

Head Office—c/o British Museum (Natural History), Cromwell Road, London, S.W.7.

Publication Office and Library—56, Queen's Gate, London, S.W.7.

CONTENTS.

PAGE

BENNETT, F. D.
Parasites of *Ancylostomia stercorea* (Zell.), (Pyralidae, Lepidoptera) a Pod Borer attacking Pigeon Pea in Trinidad (*illustrated*) .. 737

BENNETT, F. D. & HUGHES, I. W.
Biological Control of Insect Pests in Bermuda 423

BRADLEY, J. D.
A Xyloryctid Moth attacking the Bark of the Rubber Tree in Malaya (*illustrated*) 9

BREESE, M. H. & WISE, T. E.
The Biology of *Nausibius clavicornis* (Kug.) (Col., Cucujidae) (*illustrated*) 237

BRIGGS, J. B.
Three new Strains of *Amphorophora rubi* (Kalt.) on cultivated Raspberries in England 81

BROWN, E. S.
Immature Nutfall of Coconuts in the Solomon Islands. I.—Distribution of Nutfall in Relation to that of *Amblypelta* and of certain Species of Ants (*illustrated*) 97

BROWN, E. S.
Immature Nutfall of Coconuts in the Solomon Islands. II.—Changes in Ant Populations, and their Relation to Vegetation (*illustrated*) 523

BROWN, E. S.
Immature Nutfall of Coconuts in the Solomon Islands. III.—Notes on the Life-history and Biology of *Amblypelta* (*illustrated*) 559

BÜNZLI, G. H. & BÜTTIKER, W. W.
Fungous Diseases of Lamellicorn Larvae in Southern Rhodesia .. 89

BÜNZLI, G. H. & BÜTTIKER, W. W.
A Comparative Study of the Soil Conditions favoured by certain Melolonthid and Tenebrionid Pests of Tobacco in Southern Rhodesia (*illustrated*) 259

BURGES, H. D.
Studies on the Dermestid Beetle, *Trogoderma granarium* Everts. II.—The Occurrence of Diapause Larvae at a Constant Temperature, and their Behaviour (*illustrated*) 407

CARDEN, P. W.
The Control of Onion Fly, *Delia antiqua* (Mg.), with Seed Dressings (*illustrated*) 795

CASWELL, G. H.
Observations on an Abnormal Form of *Callosobruchus maculatus* (F.) (*illustrated*) 671

CHOW, C. Y., IBNOE, R. M. & SOEJOED TARKO JOSOPOERO.
Bionomics of Anopheline Mosquitos in Inland Areas of Java, with Special Reference to *Anopheles aconitus* Dön. 647

PAGE

CLARKE, K. U. & SARDESAI, J. B.
An Analysis of the Effects of Temperature upon the Growth and Reproduction of *Dysdercus fasciatus* Sign. (Hemiptera, Pyrrhocoridae) (*illustrated*) 387

COAKER, T. H.
Investigations on *Heliothis armigera* (Hb.) in Uganda (*illustrated*) 487

COURSHEE, R. J.
Drift Spraying for Vegetation Baiting (*illustrated*) 355

DAS, G. M.
Bionomics of the Tea Red Spider, *Oligonychus coffeae* (Nietner) .. 265

DAS, G. M.
Observations on the Association of Ants with Coccids of Tea (*illustrated*) 437

DAVID, W. A. L. & GARDINER, B. O. C.
The Action of the systemic Insecticide Fluoroacetamide on certain Aphids and on *Pieris brassicae* (L.) 25

EADY, R. D.
A New Genus and two New Species of Encyrtidae (Hymenoptera, Chalcidoidea) from the Banana Scab Moth, *Nacoleia octasema* (Meyr.) (*illustrated*) 667

FERNANDO, H. E.
The Susceptibility of the Rice Pentatomid Bug, *Scotinophara lurida* (Burm.), to Insecticides, and the Insecticidal Control of this Pest in Ceylon (*illustrated*) 717

FORD, J., GLASGOW, J. P., JOHNS, D. L. & WELCH, J. R.
Transect Fly-rounds in Field Studies of *Glossina* (*illustrated*) .. 275

FRYER, G.
Lunar Rhythm of Emergence, differential Behaviour of the Sexes, and other Phenomena in the African Midge, *Chironomus brevibucca* (Kieff.) (*illustrated*) 1

HADDOW, A. J.
Studies on the Biting Habits and Medical Importance of East African Mosquitos in the Genus *Aëdes*. I.—Subgenera *Aëdimorphus*, *Banksinella* and *Dunnius* (*illustrated*) 759

HANNA, A. D., HEATHERINGTON, W., MAPOTHER, H. R. & WICKENS, R.
An Investigation into the possible Control of the Mealybug Vectors of Cacao Swollen-shoot Virus by Trunk Implantation with Dimefox 209

HARRIS, K. M.
Notes on Gall Midges (Cecidomyiidae) on Nigerian Crops with a Description of a New Species of *Thomasiella* Rübsaamen (*illustrated*) 661

HOWE, R. W.
Studies on Beetles of the Family Ptinidae. XVII.—Conclusions and additional Remarks 287

JARMAN, R. T.
The Deposition of Airborne Droplets on dead House-flies (*Musca domestica* L.) (*illustrated*) 327

PAGE

JOYCE, R. J. V.
The Yield Response of Cotton in the Sudan Gezira to DDT Spray (*illustrated*) 567

KERNAGHAN, R. J. & DAVIES, J. B.
Field Trials of the Control of *Glossina palpalis* (R.-D.) by Obstructive Clearing (*illustrated*) 449

KETTLE, D. S., PARISH, R. H. & PARISH, J.
Further Observations on the Persistence of Larvicides against *Culicoides* and a Discussion on the Interpretation of Population Changes in the untreated Plots (*illustrated*) 63

LEWIS, D. J. & GARNHAM, P. C. C.
The Simuliidae (Diptera) of British Honduras (*illustrated*) .. 703

MCCLELLAND, G. A. H.
Observations on the Mosquito, *Aëdes* (*Stegomyia*) *aegypti* (L.), in East Africa. I.—The Biting Cycle in an Outdoor Population at Entebbe, Uganda (*illustrated*) 227

MCCLELLAND, G. A. H.
Observations on the Mosquito, *Aëdes* (*Stegomyia*) *aegypti* (L.), in East Africa. II.—The Biting Cycle in a Domestic Population on the Kenya Coast (*illustrated*) 687

MELLANBY, K.
Acclimatization affecting the Position of the Cold and Heat Death Points of Larvae of *Aëdes aegypti* (L.) 821

MILNE, A.
Biology and Ecology of the Garden Chafer, *Phyllopertha horticola* (L.). V.—The Flight Season: Sex Proportions 39

MILNE, A.
Biology and Ecology of the Garden Chafer, *Phyllopertha horticola* (L.). VI.—The Flight Season: Reproductive State of Females (*illustrated*) 467

NYE, I. W. B.
The Distribution of Shoot-fly Larvae (Diptera, Acalypterae) within Pasture Grasses and Cereals in England (*illustrated*) 53

PAGE, W. A.
The Ecology of *Glossina longipalpis* Wied. in Southern Nigeria (*illustrated*) 595

PAGE, W. A.
The Ecology of *Glossina palpalis* (R.-D.) in Southern Nigeria (*illustrated*) 617

PAGE, W. A.
Some observations on the *fusca* Group of Tsetse Flies (*Glossina*) in the South of Nigeria (*illustrated*) 633

PARR, H. C. M.
Studies on *Stomoxys calcitrans* (L.) in Uganda, East Africa. I.—A Method of Rearing large Numbers of *Stomoxys calcitrans* .. 165

PREVETT, P. F.
The Oviposition and Duration of Life of a small Strain of the Rice Weevil, *Calandra oryzae* (L.), in Sierra Leone (*illustrated*) .. 697

PAGE

RAW, F.
An Insectary Method for Rearing Cacao Mirids, *Distantiella theobroma* (Dist.) and *Sahlbergella singularis* Hagl. (*illustrated*) 11

RAW, F.
Studies on the Chemical Control of Cacao Mirids, *Distantiella theobroma* (Dist.) and *Sahlbergella singularis* Hagl. 13

SAYER, H. J.
An Ultra-low-volume Spraying Technique for the Control of the Desert Locust, *Schistocerca gregaria* (Forsk.) (*illustrated*) .. 371

SMITH, K. G.
Insect Infestation associated with French shelled Walnuts with particular Reference to the Occurrence of *Aphomia gularis* (Zell.) (Lep., Galleriidae) (*illustrated*) 711

SMITHERS, C. N.
Some recent Observations on *Busseola fusca* (Fuller) (Lep., Noctuidae) in Southern Rhodesia 809

SQUIRE, F. A.
Infectibility of Tsetse Flies, *Glossina palpalis* (R.-D.) and *G. tachinoides* Westw. with *Trypanosoma vivax* 183

SURTEES, G.
The Breeding Behaviour of the Type Form of *Aëdes* (*Stegomyia*) *aegypti* (L.) in south-western Nigeria in Relation to Insecticidal Control 681

SWAINE, G.
A preliminary Note on *Helopeltis* spp. damaging Cashew in Tanganyika Territory (*illustrated*) 171

SYMMONS, P.
The Effect of Climate and Weather on the Numbers of the Red Locust, *Nomadacris septemfasciata* (Serv.), in the Rukwa Valley Outbreak Area (*illustrated*) 507

SYMMONS, P. & CARNEGIE, A. J. M.
Some Factors affecting Breeding and Oviposition of the Red Locust, *Nomadacris septemfasciata* (Serv.) (*illustrated*) 333

TEESDALE, C.
Observations on the Mosquito Fauna of Mombasa (*illustrated*) .. 191

VANDERPLANK, F. L.
Studies on the Coconut Pest, *Pseudotheraptus wayi* Brown (Coreidae), in Zanzibar. II.—Some Data on the Yields of Coconuts in Relation to Damage caused by the Insect 135

VANDERPLANK, F. L.
Studies on the Coconut Pest, *Pseudotheraptus wayi* Brown (Coreidae), in Zanzibar. III.—A selective residual Insecticidal Formulation and its Effects on the Ecology of the Insect 151

WALKER, P. T.
Insecticide Studies on East African Agricultural Pests. III.—Seed Dressings for the Control of the Bean Fly, *Melanagromyza phaseoli* (Coq.), in Tanganyika (*illustrated*) 781

Dates of Publication in Parts

Part I pp. 1–226	..	25 March, 1959
Part II pp. 227–422	..	31 August, 1959
Part III pp. 423–646	..	24 November, 1959
Part IV pp. 647–824	..	13 January, 1960

Errata

Page 37, line 19, delete sentence " Fluoroacetamide . . . compounds."
Page 196, footnote to Table V, for " *Aë. cununinsi* " read " *Aë. cumminsi mediopunctatus* " and for " *C. weschei* var. *mediopunctatus* " read " *C. weschei* var. *gediensis* "
Page 199, 2nd col., for " *M. brevipalpis* " read " *Tox. brevipalpis* "
Page 224, line 5, for " (Laing) " read " Laing "
Page 284, line 10, for " 200 yd." read " 100 yd."
Page 549, line 14, for " *Oecophlla* " read " *Oecophylla* "
Page 631, line 10, for " increases " read " increase "
Page 659, line 23, for " remainder " read " 1,438 examples "
Page 659, 21 lines from end, delete " respectively "
Page 659, 2 lines from end, for " May " read " July "
Page 659, last line, for " *A. tessallatus* " read " *A. tessellatus* "
Page 684, line 15, for " numbers " read " number "
Page 689, Table I, 1st col., transpose " lateral spots silver " and " lateral spots white "
Page 709, line 15, for " 18th " read " 15th "
Page 732, line 30, for " only " read " at most "
Page 734, line 9, for " DDT " read " DDT, chlordane "
Page 734, line 10, for " about " read " at most about "
Page 734, line 11, for " 0·045 " read " 0·45 "
Page 822, 7 lines from end, for " one hour " read " 24 hours "

COMMONWEALTH INSTITUTE OF ENTOMOLOGY.

BULLETIN
OF
ENTOMOLOGICAL RESEARCH.

Vol. 50. 1959.

LUNAR RHYTHM OF EMERGENCE, DIFFERENTIAL BEHAVIOUR OF THE SEXES, AND OTHER PHENOMENA IN THE AFRICAN MIDGE, *CHIRONOMUS BREVIBUCCA* (KIEFF.).

By G. Fryer *

Northern Rhodesia–Nyasaland Joint Fisheries Research Organisation.

The midge, *Chironomus* (*Nilodorum*) *brevibucca* (Kieff.), is apparently common and widespread in East and Central Africa. In Lake Bangweulu, Northern Rhodesia, it is extremely common. Here, preliminary observations have shown that its larvae occur as bottom dwellers in the sandy littoral region of the lake, where they constitute the dominant and indeed almost the sole Chironomid species of the benthos; but apparently they do not occur to any extent in the mud of deeper water. These larvae probably constitute the most important single item of food of the fishes of the lake, for the guts of many fishes belonging to various species, and including several which are much valued as human food, have frequently been seen crammed with larvae, and at times pupae, of this species, to the exclusion of all other food.

Lunar Rhythm of Emergence.

Chironomus brevibucca exhibits the phenomena of mass emergence and lunar periodicity. Observations around Lake Bangweulu in 1956 indicated that mass emergence takes place shortly after the appearance of a full moon, that the peak period of emergence is from three to five days after the full moon, and that the main season of emergence is from June or July to October or November, *i.e.*, in the period of increasing temperature preceding the rains. Further data on seasonal phenomena are needed as observations had of necessity to be intermittent, but it may be noted that scarcely a single imago was to be found during February 1957.

* Present address: East African Fisheries Research Organisation, P.O. Box 343, Jinja, Uganda.

Strictly quantitative data on emergence and abundance have not been collected, but from events which took place in August and September, when uninterrupted observation on several nights was possible, supplemented by several observations in July, it appears that, after a period when no midges are to be found, moderate numbers appear on two successive nights (nights 1 and 2 after full moon in August, and nights 2 and 3 in September) to be followed by vast swarms on the following night. The latter are present for three nights, then numbers gradually diminish so that seven nights after the first appearance of swarms only stragglers are left and even these are not to be found three or four nights later.

Useful evidence that this species does indeed exhibit a true lunar rhythm of emergence was provided by a large sample collected in the same area one day after the appearance of a full moon in July 1953 by Mr. D. Harding.

At peak periods of emergence, imagines occur in countless millions, so much so that houses near the lake shore have to be screened to prevent their entry.

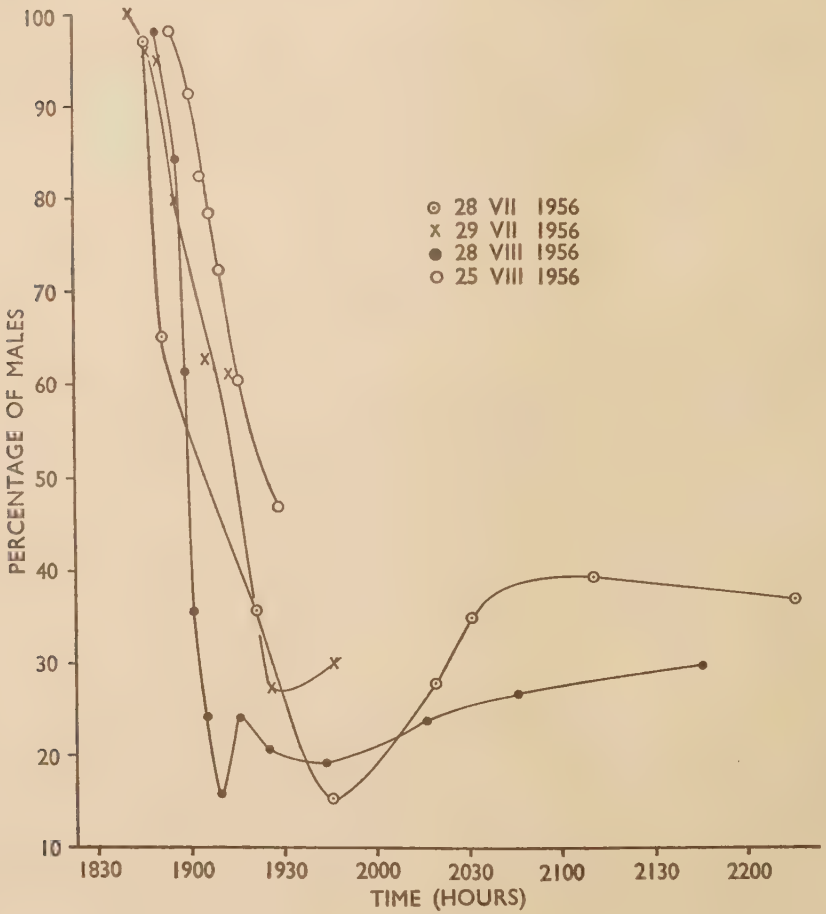


Fig. 1.—Change in sex ratio with time, of individuals of *Chironomus brevibucca* attracted to light. (Some of the early counts at the upper end of the graph are omitted for clarity.)

Attracted by light, imagines fly to these gauze screens which, at peak periods of emergence, become covered with a solid mass of midges. On days following such nights, bucketfuls of midges can be scooped from beneath the screens, and pupal skins are washed on to the lake shore in such numbers as to form solid mats near the water line. Between peaks of emergence, that is, in periods between full moons, there are many nights when the screens are completely free of midges.

Differential Behaviour of the Sexes.

Interest in sex ratios was first aroused when it was noticed that among midges remaining on a gauze screen on the day following a night's swarming there was a marked preponderance of females, while on several adjoining whitewashed walls males were present in greater numbers than females. Four random samples from screens, totalling 1,322 insects, showed that females exceeded males by about 4·68:1. On walls, 26 random samples, on various dates, totalling 7,389 insects, revealed that, on average, 2·92 males were present for each female. In one exceptional sample, 176 females were counted in company with 153 males, but in all others males preponderated, and in some cases, as where 400 males were accompanied by only 4 females and when 532 males occurred with 8 females, the disparity in numbers between the sexes was most striking.

In a rather small sample collected from grasses near the lake margin, 108 females occurred with 13 males. Here the disparity may be explained if the females represented individuals that had oviposited and then flown back to shore to rest and die.

This phenomenon, while interesting, is by no means so remarkable as the change in sex ratio that takes place over an interval of a few minutes during the period shortly after the fall of darkness when the insects begin to collect near sources of light. Observations on this behaviour were made on the screens of a house facing the lake, some 150 yd. from the shore and about 120 ft. above the lake surface. The source of illumination was a paraffin lamp of the pressure type used for household lighting. The lamp stood about 5 yd. from the gauze screen and between the two was a moderately thick cotton curtain. The illumination was therefore very diffuse and not very intense.

Typically, the following sequence of events takes place. The first flies to come to the screens are almost invariably males, but after a few minutes females appear, rapidly increase in numbers so as to usurp the dominant position occupied by the males, and finally to constitute the bulk of the population on the screen. Examples of this remarkable change in sex ratio in relation to time are shown in fig. 1.

The times quoted are local (South African) time which is two hours ahead of G.M.T. The graphs were plotted from random counts made from outside the screens. From this vantage point the insects could be seen silhouetted against the light and the sexes could be readily distinguished. To give some idea of the numbers usually involved in the counts, Table I gives the figures obtained on the night of 24th August 1956.

On two occasions, behaviour was somewhat atypical in that the percentage of males did not fall as low as usual, and this is shown in fig. 2. In one of these cases (23rd August 1956) very few insects were present, this being the night before the peak of that month's emergence. In spite of the fact that on these two nights the females never achieved the preponderance that they did on typical nights, the shape of the curves is still the same and in each case the proportion of males showed a sharp decline during the early part of the movement towards the light.

A "kink" at the time when the percentage of males is at a minimum

TABLE I.

Numerical data showing change in sex ratio with time, of individuals of *Chironomus brevibucca* attracted to light on the night of 24th August 1956.

Time	No. of males	No. of females	Percentage of males
1844 ..	62	3	95·4
1846 ..	110	1	99·1
1849 ..	174	3	98·3
1852 ..	176	2	98·9
1855 ..	80	15	84·2
1858 ..	100	63	61·4
1901 ..	53	96	35·6
1905 ..	46	143	24·3
1909 ..	39	209	15·7
1915 ..	53	166	24·2
1925 ..	48	177	21·3
1943 ..	38	160	19·2
2015 ..	65	208	23·8
2045 ..	58	163	26·2
2145 ..	91	218	29·5

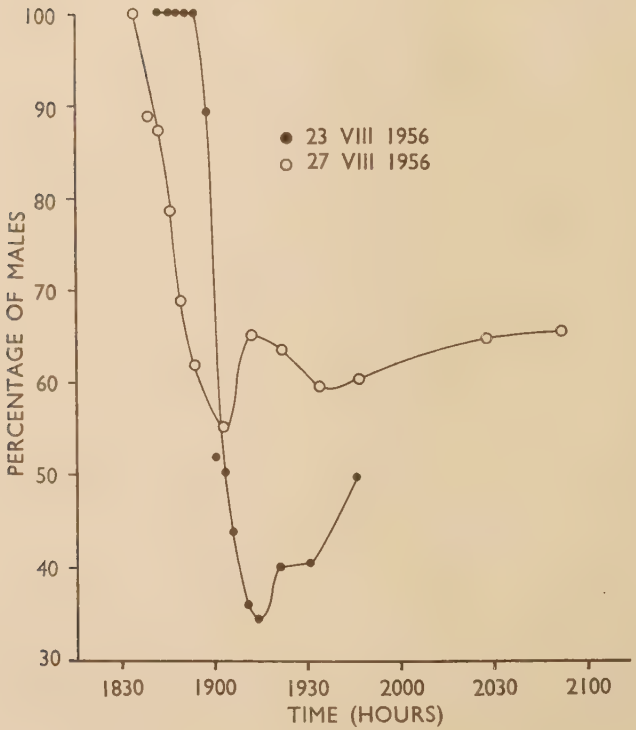


Fig. 2.—Change in sex ratio with time, of individuals of *Chironomus brevibucca* attracted to light—the examples of slightly atypical behaviour mentioned in the text.

appears to be a regular feature of the graphs and seems to indicate that a secondary influx of males takes place when certain conditions are fulfilled. Observations on the condition of the antennae (see below) suggest, however, that this is not due to males emerging about that time and arriving shortly afterwards at the screens as they undoubtedly do during the early nights of an emergence period.

While some of the flies which swarm to the light have almost certainly come directly there after emergence from the lake this does not appear to be true for the majority. During the early nights of emergence some of the males seen on the screen have wet and " unfeathered " antennae. When such males are placed in a tube their antennae dry and become " feathered " within 15 to 30 minutes. It is presumed that such males have just emerged from the lake. On the later nights of swarming no such males have been observed. It is assumed, therefore, that most of the insects on the screens have an adult age of at least one day. It is interesting to note that although the midges on the screens on the earlier days of a swarming period include newly emerged insects the general pattern of events is the same on all nights.

Evidence was obtained that males sometimes leave the screens after settling there. The first night of swarming for that particular emergence period was 22nd September 1956, and the number of midges at the screen was small. At 1847 hours, 48 males and one female were present, but by 1935 hours only 12 males were present on the entire screen, showing that some individuals of this sex must have departed.

Miscellaneous Observations.

A few scattered observations on *C. brevibucca* which cannot at present be co-ordinated are worthy of brief mention. There is a very restricted period of intense flight activity in the evening at twilight, very roughly 25 to 35 minutes before the midges begin to congregate at sources of light, when they form themselves into compact and continually moving swarms, usually over bushes or small trees. From the time that these swarms begin to congregate until the disappearance of the last stragglers only about 20 minutes elapse, and most activity is concentrated into a period of less than 15 minutes. Activity ceases just before the light intensity falls to a level at which it is impossible to read a page of newsprint. Insects leaving the swarms settle on walls and vegetation. While, very occasionally, pairs of midges have been observed in such swarms, most of the insects comprising them are males. Almost all those captured in nets from such swarms were males and the same applies to the thousands of midges that settled on the walls of the house after leaving the swarms and were readily observed. It would appear that the males indulging in this activity had an adult age of at least one day as they had fully " feathered " antennae, and no evidence of emergence and flight by day was obtained.

Mass movements of females (accompanied by some males) were also noticed on two occasions at dusk during the period of flight activity. These insects were moving in a band at a brisk human walking speed over a wide earth road and its margins. They formed a layer, commencing about five ft. above the road, several yd. deep and at least 20 yd. wide and must have numbered millions. This band passed steadily for at least 20 minutes on one occasion and became thinner and finally dispersed just before complete darkness. A net sample from this swarm produced 498 females and 40 males.

On another occasion, several swarms of fairly lazily flying males were observed over the road at dusk and at the same time a few females were moving steadily along the road independently of the males. The significance of these movements is not known.

It is not known whether *C. brevibucca* has a period of morning activity corresponding to that taking place in the evening, as have certain European Chironomids (Williams, 1935, 1936). However, the fact that females outnumber males on the screens by day while males are more abundant elsewhere suggests that some females, after being attracted to the screens in the evening, do not leave them again until the following evening.

While most of the midges seen by day are resting on vegetation or walls, some diurnal activity has been observed on the lake shore. In the forenoon of 28th August 1956, when the vegetation near the water's edge was clothed with millions of midges, considerable numbers of both sexes were seen moving out from the shore over the water and were noticed at distances of at least 30 yd. from the shore. Some of the females were observed fluttering over the water surface and were possibly ovipositing. (Egg clusters of a Chironomid—by inference of this species—were very plentiful in the marginal waters.) Even so, by comparison with the number of resting insects the number seen over the water was quite small and those seen may have been disturbed individuals that had flown over the water where, obviously, they could not settle as would be the case on shore.

Discussion.

As emergence is cyclical and there are times between periods of emergence when no midges are to be found, it is apparent that the duration of adult life is certainly not more than ten days and is usually much less than this.

Further observations on the incidence of this species are needed during the months when no mass emergence was recorded. If the absence of adults at this time of the year is confirmed, then this species must have a longer life-cycle than that demonstrated for some tropical African Chironomids by Macdonald (1956).

That emergence of this species is associated with the time of full moon, or just after it, is of interest partly because very few cases of lunar periodicity in non-marine organisms are known, and partly because the time of emergence in relation to moon age is similar to that of what is perhaps the best authenticated of these cases—that of the mayfly, *Povilla adusta* Navás (Hartland-Rowe, 1955).

It is also of great interest to note that, among marine organisms (essentially polychaete worms) exhibiting once-monthly lunar rhythms of spawning and swarming, the times of such phenomena in relation to moon age are similar to those found in *C. brevibucca*. (See Korringa, 1957, for a general review.)

Korringa (1957) seeks to explain these phenomena, which have proved an enigma to marine biologists for well over half a century, by putting forward a hypothesis which, if correct, would also apply to *C. brevibucca*. As it would appear that no attempt has been made to explain lunar periodicity in non-marine organisms it is worth while briefly considering Korringa's hypothesis and its applicability in the present case.

All the polychaetes that swarm just after full moon live in shallow water where the effects of light can operate. So do the larvae of *C. brevibucca* (p. 1). By day the polychaetes are hidden in various ways and emerge to seek food only at night. By day the larvae of *C. brevibucca* definitely live buried in the sand, and therefore shielded from light, and may well emerge to forage by night. Were this not the case it is hard to imagine how such a fish as *Chrysichthys mabusi*, which feeds on them extensively, could collect them. An exactly similar diurnal rhythm has been shown to take place in *Povilla adusta*, which also exhibits a similar lunar periodicity (Hartland-Rowe, 1955). Korringa suggests that during the period of nocturnal exposure the organisms respond to the rhythmic alternation of dark and moonlight nights in a similar manner to the

well-known response in sexual and migratory activities of birds to rhythmical differences in illumination—the lengthening and shortening of days. (Many plants are also sensitive to day length, and more to the duration of the period of illumination than to the intensity of the light.) If, during the breeding season, the ripening of the gonads is initiated by nocturnal illumination, then the completion of maturation, resulting in swarming, could reasonably be expected during the period of a waxing moon. This theory seems to explain the periodic swarming of these polychaetes just after the time of full moon as being the result of an additive effect of exposure to nocturnal illumination on the maturation of organisms that are not subjected to sunlight by day. It requires no reference to any of the far-fetched and sometimes fantastic suggestions which have been put forward in the past, and there appear to be no formidable obstacles in the way of its explaining the emergence behaviour of *Chironomus brevibucca* and *P. adusta*.

Attention may be directed emphatically to the fact that these insects provided material that is much more amenable to experiment for the checking of this hypothesis than are most of the marine organisms to which it has been applied.

Dr. P. S. Corbet informs me that he collected specimens of *C. brevibucca* from a swarm near the Equator in Uganda in July 1957, seven days after *new* moon. It seems likely, therefore, that the same species may have different swarming habits in different areas or may exist in different biological races. Similar problems are posed by certain polychaetes, which show different rhythms in different areas.

While it is important to distinguish clearly between lunar effects on emergence and activity it may be noted that in *C. brevibucca* the two periods inevitably coincide. (This is by no means certain to be the case in longer-lived insects.) Thus, while the comparison is perhaps somewhat equivocal, it may be pointed out that such behaviour stands in contradistinction to the results recently obtained in England by Williams, Singh & el Ziady (1956) which revealed no evidence of lunar rhythms of activity in various groups of insects; the rhythm of Noctuid moths with a peak of activity near the time of the new moon, apparently demonstrated by the earlier work of Williams (1935, 1936), was in fact shown to be an artefact resulting from the sampling technique employed.

When discussing the lunar rhythm of emergence of *Povilla adusta*, Hartland-Rowe (1955) suggested that it was possible that a lunar rhythm is only maintained near the Equator where the annual variation in day length and temperature is low, though he admitted that his evidence was meagre. As the locality in which the present observations were made is more than 11° south of the Equator and distinct seasons are experienced, the indications are that lunar rhythms are to some extent independent of changing climatic conditions, as they appear to be in the sea.

Summary.

Larvae of the African midge, *Chironomus brevibucca* (Kieff.), are abundant in the littoral zone of Lake Bangweulu, Northern Rhodesia, where, at certain times of the year, imagines emerge in vast numbers shortly after the appearance of the full moon. Attracted by light, the imagines fly to houses and alight on the protective gauze screenings, which, at peak periods of emergence, become covered with a solid mass of midges. They have not been seen at other phases of the lunar cycle, so the adult life is certainly not more than ten days and is usually much less.

Imagines, which are inactive by day, tend to settle in different situations according to their sex. On the gauze screenings there was a marked preponderance of females (4·68 : 1) on the day following a night's swarming but, on

several adjoining whitewashed walls, males predominated (2·92 : 1). On grasses near the lake margin females outnumbered the males.

When the gauze screening of a house was diffusely illuminated, imagines were attracted to it during the early hours of darkness. The first flies to arrive were almost invariably males, but females followed on rapidly and finally constituted the bulk of the population. On one evening the percentage of males fell in three hours from 95·4 at 1844 hr. to 29·5 at 2145 hr. The percentage of males reaches a minimum between 1900 and 2000 hr. and thereafter shows some rise, probably due to a secondary influx of males which are thought to have been resting during the day and not to be newly emerged.

An indication of the adult age of males seems to be given by the condition of the antennae during the early part of their adult life.

Some miscellaneous observations on the behaviour of *C. brevibucca* are recorded.

Some aspects of the phenomena recorded are discussed. The recent hypothesis of Korringa, which seeks to explain the periodic swarming of certain polychaetes just after the time of full moon as being the result of an additive effect of exposure to nocturnal illumination on the maturation of organisms that are not subjected to sunlight by day, is examined and shown to be applicable to *C. brevibucca*.

Acknowledgements.

My thanks are due to Mr. P. Freeman who identified the insect concerned, and to Dr. P. S. Corbet for much appreciated criticism of the text.

References.

Hartland-Rowe, R. (1955). Lunar rhythm in the emergence of an Ephemeropteran.—*Nature, Lond.* **176** p. 657.

Korringa, P. (1957). Lunar periodicity.—*Mem. geol. Soc. Amer.* no. 67 pt. 1 pp. 917–934.

Macdonald, W. W. (1956). Observations on the biology of Chaoborids and Chironomids in Lake Victoria and on the feeding habits of the "elephant-snout fish" (*Mormyrus kannume* Forsk.).—*J. Anim. Ecol.* **25** pp. 36–53.

Williams, C. B. (1935). The times of activity of certain nocturnal insects, chiefly Lepidoptera, as indicated by a light-trap.—*Trans. R. ent. Soc. Lond.* **83** pp. 523–555.

Williams, C. B. (1936). The influence of moonlight on the activity of certain nocturnal insects, particularly of the family Noctuidae, as indicated by a light trap.—*Phil. Trans.* (B) **226** pp. 357–389.

Williams, C. B., Singh, B. P. & el Ziady, S. (1956). An investigation into the possible effects of moonlight on the activity of insects in the field.—*Proc. R. ent. Soc. Lond.* (A) **31** pp. 135–144.

© Commonwealth Agricultural Bureaux, 1959.

A XYLORYCTID MOTH ATTACKING THE BARK OF THE RUBBER TREE IN MALAYA.

By J. D. Bradley

Department of Entomology, British Museum (Natural History).

An infestation by Lepidopterous larvae feeding on the outer bark of rubber trees, *Hevea brasiliensis*, has been reported on an estate in the coastal district of Selangor, Malaya (*Bull. Rubb. Inst. Malaya* no. 35 p. 44, 1958). Efforts to identify the species were unsuccessful at that time and it was believed to be an undescribed member of the genus *Ptochoryctis* Meyrick, belonging to the family Xyloryctidae.* It has, however, now been determined as *Deloryctis corticivora* Meyrick, a species described from Java, where the larva feeds on the bark of Ceylon oak, *Schleichera trijuga*, and so far as is known not previously recorded from Malaya.

The species is redescribed below from female examples received from Dr. A. Newsam, of the Rubber Research Institute, Malaya.



Figs. 1–2.—*Deloryctis corticivora* Meyrick. (1) Left-hand wings. (2) Ventral view of female genitalia.

* This paper was originally intended to describe the species as new and was in press when the determination was made.

Deloryctis corticivora Meyrick, 1934, Exotic Microlepidoptera **4** p. 464. (Figs. 1 & 2.)

♀. Expanse 18–20 mm. Labial palpus ochreous suffused with greyish fuscous except basal segment, which is overlaid with whitish. Head, thorax, patagium and tegula white. Antenna fuscous with a narrow whitish-ochreous medial line on the underside extending to about $\frac{3}{4}$, scape white. Forewing white, a large almost solid dark brown blotch weakly irrorate with ochreous and with an admixture of a few white scales, more especially in the distal portion, rising from dorsum (inner margin) at $\frac{1}{3}$ and occupying most of the distal two-thirds of the wing except for a narrow margin along the costa and around the apex, inner edge of blotch straight and directly transverse to middle of wing, thence curved and oblique to termen a little below the apex, a conspicuous white pretornal spot extending into cilia; cilia white, a thin dark brown medial line well defined around apex and along termen to middle, thence rather diffuse to tornus, apices of cilia suffused with greyish pale ochreous. Hind wing greyish pale ochreous, lighter proximally, cilia white. Abdomen white. Legs white, foreleg heavily suffused with fuscous, tarsi of middle and hind legs suffused with light fuscous.

Female genitalia (fig. 2): Ostium entrance circular, leading to a moderately well sclerotised cylindrical tube. Ductus bursa narrow, broadening a little about midway to bursa copulatrix. Signum present, irregular in shape with poorly defined margins but roughly circular, traversed by a narrow well sclerotised keel-like ridge.

♂. This may be slightly smaller but otherwise only differs from the female superficially in having the apical area of the hind wing suffused with brown. The genitalia of this sex are figured by J. F. Gates Clarke (1955, Catalogue of the Type Specimens of Microlepidoptera in the British Museum (Natural History) described by Edward Meyrick **2** pl. 209).

Deloryctis corticivora is the sole representative of the genus and its nearest relative appears to be *Ptochoryctis chalazopa* Meyrick, which occurs, so far as is known, only in Indonesia (Java) and is likewise a bark-feeder on rubber. The two species are similar superficially but in *chalazopa* the dark brown marking on the forewing rises from the dorsum nearer the base and is not as solid as in *corticivora*. The female genitalia are also very similar but in *chalazopa* the ostium entrance is slightly narrower and the initial sclerotised portion is longer than in *corticivora*; in *chalazopa* the bursa copulatrix lacks a signum.

The illustration of the wings in fig. 1 is from a drawing by Mr. Arthur Smith.

© Commonwealth Agricultural Bureaux, 1959.

AN INSECTARY METHOD FOR REARING CACAO MIRIDS, *DISTANTIELLA THEOBROMA* (DIST.) AND *SAHLBERGELLA SINGULARIS* HAGL.

By F. Raw *

West African Cocoa Research Institute, Tafo, Ghana.

(Plate I.)

During investigations on the chemical control of *Distantiella theobroma* (Dist.) and *Sahlbergella singularis* Hagl., two species of Mirid injurious to cacao in West Africa, a supply of adults and nymphs was required for experimental work. Hand-collecting in the bush was tedious and could not be relied upon for regular supplies. The insects are soft-bodied, the antennae and legs are particularly fragile, and all stages, especially the early ones, are easily damaged by handling. Consequently, many individuals laboriously collected in the field could not be used for experiments. The age of the adults and the general condition of field material varied and was likely to affect results. To overcome these difficulties, a method for rearing from egg to adult in the insectary was developed.

Life-cycle of *D. theobroma* and *S. singularis*.

There are only minor differences in the life-cycles of the two species and they do not affect the method used to rear the insects. On cacao, the eggs are laid singly, or occasionally in pairs, in the pod cortex or beneath the epidermis of unhardened, or recently hardened, chupons and fans. Only a pair of fine terminal filaments protrudes from the surface. The incubation period is about 17 days. There are five nymphal instars, each requiring 3–5 days for completion. Adults and nymphs feed mainly on green unhardened tissue such as unripe pods and chupon or fan flushes. Females begin to lay eggs about a week after emergence and may lay 30–40 eggs each. The adults live for about three weeks but there is a great variability in both fecundity and length of life.

Insectary Method for Rearing *D. theobroma* and *S. singularis*.

This was carried out in two stages, the production and incubation of eggs and rearing nymphs and adults.

Production and incubation of eggs.

Eggs were obtained by caging gravid females on cacao seedlings grown in baskets (Pl. I, fig. 1). For this purpose well grown Amelanado seedlings 6–9 months old were found to be most suitable. It was convenient to maintain a supply of these in a seedling nursery and to select for use those which had an unhardened and a recently hardened flush to provide feeding and oviposition sites for the caged females. The cages were sleeves of mosquito netting supported on two cane rings of about 8 in. diameter. They could be slipped over the seedling and fastened round the stem at top and bottom. Two or three gravid females were caged on each seedling at a time. At 24-hr. intervals the stem was examined, under a hand lens, for eggs until about 20 eggs had been deposited

* Seconded from Rothamsted Experimental Station, Harpenden, Herts.

or until it was felt that the seedling would be harmed by more feeding. Each seedling was labelled with the date and number of eggs laid on it and then kept in a shaded insectary or palm-thatched shelter until the eggs began to hatch. Each seedling was grease-banded near the base to prevent infestation by ants or other potential predators.

Rearing nymphs and adults.

After 14 days' incubation, each seedling was searched twice daily for newly emerged nymphs. These were picked off with a soft sable brush into petri dishes containing pieces of chupon and then transferred to unripe pods suspended in the rearing cages. These were set up as shown in Plate I, fig. 2.

Each cage consisted of a wide lamp glass with a piece of aluminium strip bent to clip across the top. An unripe pod was suspended in the cage using a paper clip, one end of which gripped the pod stalk while the other was hooked over the aluminium strip. Although nymphs were susceptible to desiccation, experience showed that through ventilation was necessary to prevent harmful condensation. This was satisfactorily achieved by covering the bottom of the lamp glass with loosely woven calico and the top with mosquito netting and then supporting each cage in a circular hole of the required diameter in a raised platform.

The pods wilted and had to be replaced every 4–5 days. For economy, each pod was given as many nymphs as it could sustain for this time, usually 25–30 first- or second-instar nymphs or about five fifth-instar nymphs or adults. When numbers were regulated in this way each pod sufficed for about the duration of each instar.

Discussion.

Adults mated and oviposited readily in the rearing cages, which were well suited to observe this. Unsuccessful attempts were made to maintain the pods sufficiently long for these eggs to hatch and so obviate the use of basket seedlings for oviposition. Wilting could be delayed by supplying nutrient solution to the pods through the stalk but it was found that the pods invariably succumbed to bacterial or fungal rots after 10 days or so and further attempts to hatch eggs laid in pods were abandoned.

Summary.

An insectary method for rearing the cacao Mirids, *Distantiella theobroma* (Dist.) and *Sahlbergella singularis* Hagl., is described. Adults are caged, for oviposition, on cacao seedlings grown in baskets. When the eggs hatch, the nymphs are transferred to, and reared on, unripe pods suspended in ventilated glass cages.

© Commonwealth Agricultural Bureaux, 1959.



FIG. 1. Inspecting a cacao seedling for Mirid eggs after adults had been caged on it.



FIG. 2. Cages for rearing cacao Mirids on unripe cacao pods. These show feeding lesions.

INSECTARY METHOD OF REARING *D. THEOBROMA* AND *S. SINGULARIS*.

STUDIES ON THE CHEMICAL CONTROL OF CACAO MIRIDS, *DISTANTIELLA THEOBROMA* (DIST.) AND *SAHLBERGELLA SINGULARIS* HAGL.

By F. Raw *

West African Cocoa Research Institute, Tafo, Ghana.

In West Africa, four species of Mirid, *Distantiella theobroma* (Dist.), *Sahlbergella singularis* Hagl., *Bryocoropsis laticollis* Schum., and *Helopeltis bergrothi* Reut., are pests of cacao. *B. laticollis* and *H. bergrothi*, which are less common than the others, are largely confined to the pods and seem to do little damage. *D. theobroma* and *S. singularis*, which feed on young vegetative growth as well as on pods, do such damage that they are considered important factors limiting cocoa production in West Africa.

Both species are typical plant-feeding Heteroptera. They breed continuously and all stages occur on cacao throughout the year, though in Ghana they are usually most abundant from December–February and least so from March–May. Their habits and life-history were investigated by Cotterell (1926). The eggs are inserted beneath the epidermis of pods and shoots, with only a pair of filaments projecting from the surface, and they hatch in about 17 days. There are five nymphal instars, each lasting 3–5 days. Females begin to lay eggs about a week after emergence and may lay 30–40 eggs each. Adults live for about 3 weeks but fecundity and length of life vary greatly.

Nymphs and adults feed mainly on green unhardened tissue such as unripe pods and chupon and fan flushes and cause two kinds of damage. Primary damage, characterised by depressed blackened lesions surrounding the feeding punctures, results from the histolytic action of saliva injected during feeding (Goodchild, 1952). Secondary damage, characterised by canker and die-back, occurs when the lesions are invaded by the fungus, *Calonectria rigidiuscula*, a secondary parasite. Crowdy (1947) showed that much of the die-back formerly attributed to direct Mirid attack was caused by the fungus.

Primary damage, when severe, retards vegetative growth of mature trees and stunts and delays fruiting in younger trees. Seedling cacao is more susceptible and a plant may be killed before the first jorquette is formed if the attack is persistent and lesions encircle the stem. Die-back, caused by *Calonectria* infection, aggravates the effects of primary damage, progressively affects the crown of mature trees and may even kill them. Under natural conditions, secondary infections by *Calonectria* appear to be very common, and Mirid attack is usually followed sooner or later by canker and die-back. The effects of Mirid attack alone can be severe; combined with *Calonectria* infection it has caused widespread devastation in West African cacao.

Taylor (1954) has summarised the results of previous investigations, including those on chemical control, in Ghana. Dudgeon (1910) recommended spraying with kerosene emulsion but this had a low toxicity. Cotterell (1943) tested nicotine sulphate, lime sulphur and Tropical Mortegg and found the first was effective at a concentration of 1 in 1,000 and the last two caused leaf scorch even at low concentrations. However, the high mammalian toxicity of nicotine sulphate, which makes application difficult and dangerous, and its high cost, preclude its widespread use. When DDT and BHC became available they were

* Seconded from Rothamsted Experimental Station, Harpenden, Herts.

tested. Preliminary laboratory experiments showed that DDT was toxic to nymphs and adults but acted rather slowly (Anon., 1951). BHC smokes were more effective than DDT smokes (Anon., 1953). Blocks of cacao damaged by Mirids were treated with 2·5 per cent. technical DDT and the effectiveness of control was assessed by counting Mirids and estimating new damage at regular intervals afterwards. Mirid populations were reduced and damage arrested, sometimes for six months after treatment, and it was concluded that this was due to the persistence of DDT (Anon., 1949). Later, sprays containing 2·5 or 1·25 per cent. technical DDT, or 0·06 or 0·03 per cent. γ BHC were tested (Anon., 1951, 1954). All reduced Mirid populations and damage, but pronounced differences between treatments were not detected (Anon., 1955).

From the results of the trials with DDT it was recommended that, to control Mirids on seedling cacao, treatment should be applied each year, in February, June–July and November (Taylor, 1954). Later, spray painting was recommended for young and intermediate cacao. To economise on materials and time it was recommended that spraying should be limited to strategic parts of the trees, such as branch unions and jorquettes where Mirids rested (spray painting), instead of covering the whole and wasting spray.

However, the difficulties in spraying cacao limited the extent to which these recommendations could be applied. In West Africa, cacao is grown under natural forest shade and is irregularly spaced. In these conditions only portable spraying and dusting machinery can be used and, until power-driven portable sprayers of the "Kiekens Decker" and "Mist blower" type were introduced, portable sprayers could not effectively spray mature cacao, which may be up to 35 ft. high; for mature cacao, DDT dusts were tested and recommended. When power-driven portable sprayers were introduced, spraying, in the form of a mist, was extended to mature cacao (Anon., 1955).

The investigations described here, which have already been briefly reported (Anon., 1957*a*, pp. 49–50), were done primarily to provide information on some of the more urgent problems of chemical control which had arisen from previous investigations and control methods.

Experience showed that three treatments per year with 2·5 per cent. DDT did not always succeed in controlling Mirids and, particularly, they failed to protect small areas of young cacao surrounded by infested mature cacao. To protect such areas, the Ghana Department of Agriculture recommended monthly treatment. Some explanation was sought for the failure of the treatment previously recommended. Field trials had provided inconclusive evidence as to the relative merits of DDT and BHC, although it seemed probable that they differed in their toxicity to Mirids and in their mode of action. Further investigation of their merits was required, more particularly because all insecticides had to be specially imported and because a simple control policy, based if possible on the use of one insecticide, was desirable.

The evidence that DDT spray deposits persisted and remained toxic for up to six months was, at best, indirect. No direct estimates of residual toxicity had been made and it seemed more probable that DDT did not persist very long and that the length of time that sprayed cacao remained free from damage was determined by the rate of reinfestation, which would depend, among other factors, on the size of the area sprayed. To begin with, some aspects of the toxicity, mode of action, and persistence of DDT, and of BHC, were investigated. Later, preliminary tests with other insecticides were made and an account of these is given with that of the main work on DDT and BHC.

Materials.

It is difficult to carry out laboratory experiments with Mirids. They are easily damaged by handling and cannot be kept for long under artificial conditions.

Adequate numbers are difficult to obtain by hand-collecting in the bush and specimens collected in this way tend to give inconsistent results and high control mortality. To overcome some of these difficulties a method was developed for rearing them in the insectary (Raw, 1959). All the first- and second-instar nymphs used as test insects were reared in this way. Sometimes it was necessary to supplement the supply of fifth-instar nymphs and adults. The most satisfactory way to do this was to rear them in the insectary from third- and fourth-instar nymphs collected in the bush. When wild specimens had to be used for tests, they were always kept in breeding cages in the insectary for at least 24 hours and usually 48 hours beforehand.

The insects reared in the insectary proved satisfactory for tests and greatly facilitated experimental work. Even so, results were occasionally vitiated by many of the controls dying, and the supply of test insects was always a limiting factor.

At Tafo, as *D. theobroma* was more common than *S. singularis*, many more specimens of *D. theobroma* were reared. For this reason, *D. theobroma* was used for most tests, but sufficient tests were made with *S. singularis* to show that it responded to DDT and BHC very similarly.

It was found convenient to use *Tribolium castaneum* (Hbst.), a much more readily available insect, in some of the persistence tests. The beetles were reared at 30°C. on wholemeal flour under standardised conditions and were used when 2–3 weeks old.

The insecticides used were proprietary brands supplied as emulsion concentrates. Each was diluted with water to the appropriate concentration just before use. DDT and BHC were tested at concentrations used in field trials with mist sprays (Hammond, 1957) or for routine Mirid control measures. The other insecticides, which had not been used in Mirid trials previously, were tested at concentrations which were thought likely to be effective and comparable with DDT and BHC.

Experimental Methods.

Toxicity tests (contact and fumigant, if any).

Cacao Mirids cannot be kept for long without food, so all tests were made on cacao pods. There were no facilities for applying an even deposit of insecticide of known concentration to the pod surface so a more empirical method was used. Pods were sprayed to drip point or dipped in an insecticide of known concentration and the deposit was allowed to dry. The pod was suspended by its stalk in a tall beaker or wide glass chimney, and a layer of grease-banding was put round the pod below the stalk attachment to confine the Mirids to the sides of the pod, where the spray deposit was reasonably even.

For each treatment, replicated tests using five nymphs per pod were made, to reduce variability. Control tests were made, using unsprayed pods, and results were corrected for control mortality. Two kinds of tests were made.

Knockdown tests.—Nymphs were placed on the pods and the number which fell off in successive intervals was recorded. These tests were particularly suitable for first- and second-instar nymphs which showed very little tendency to fall off the control pods even when disturbed. Their normal reaction to disturbance was to run to the opposite side of the pod. Preliminary tests showed that nymphs rarely recovered after they fell from treated pods. Knockdown tests were less suitable for the fifth-instar nymphs which showed some tendency to fall off the pods when disturbed.

Exposure tests.—Nymphs were placed on the pods for a test period and then kept in petri dishes with green shoots as food for 24 hours before assessment of the kill.

Tests for fumigant action.

The fumigant action of the insecticides was tested by spraying mature cacao leaves to drip point with the test insecticide and then allowing it to dry. A disc of 3-in. diameter was then cut from the sprayed leaf and placed in the bottom of a petri dish. The test insects were confined in glass breeding cages (lamp glasses, see Raw, 1959) which were of the same diameter at the bottom as the petri dishes and which were covered, top and bottom, with mosquito netting. Second-instar nymphs were placed on pods suspended in the cages. Fifth-instar nymphs and adults were placed on pieces of green shoot. The cages were then placed on the petri dishes containing the sprayed leaf disc. With second-instar nymphs, the number which fell from the pods in successive intervals was recorded. With fifth-instar nymphs and adults, the cages were removed after exposure for a fixed time and the kill assessed 24 hours later. The tests were made at room temperature. This was consistently 28–30°C. for exposures up to 4 hours and never fell below 23°C. during exposures of 20 hours.

Tests for residual toxicity.

Tests were made using Mirids and adults of *Tribolium castaneum* as test insects.

Tests with Mirids.—Pods on trees growing under normal shade were sprayed to drip point with the insecticides to be tested. At regular intervals, a proportion of the pods was collected (usually 8 for each insecticide) and the toxicity of the residual deposit on each pod was assayed by exposure tests with Mirid nymphs.

Tests with Tribolium castaneum.—A similar procedure was followed except that mature cacao leaves were sprayed with the test insecticides. At regular intervals, eight leaves from each insecticide treatment were collected and the deposit on each leaf was assayed in the following way. Twenty adults of *T. castaneum* were counted into a 3-in. petri dish. The cacao leaf was placed over

TABLE I.

Toxicity of γ BHC and technical DDT to first-instar nymphs of *D. theobroma* and *S. singularis*.

Percentage knocked down in successive intervals when exposed on pods sprayed either 1 hour or 24 hours previously.

Interval between spraying and exposure (hr.)	Concentration of insecticide (%)	Species	No. used	Exposure (hr.)									
				¼	½	¾	1	1½	2	3	4	5	6
1	2·5 DDT	*D. theobroma*	40	—	8	—	27	40	58	100	—	—	—
	0·25 BHC		40	43	100	—	—	—	—	—	—	—	—
	0·25 BHC	*S. singularis*	37	47	86	100	—	—	—	—	—	—	—
24	2·5 DDT	*D. theobroma*	40	—	0	—	0	0	0	5	45	54	65
	0·25 BHC		38	—	15	—	45	70	87	100	—	—	—
	0·125 BHC		40	—	10	—	30	75	100	—	—	—	—
	0·25 BHC	*S. singularis*	30	—	33	—	70	80	93	100	—	—	—
	0·125 BHC		30	—	0	—	43	67	83	100	—	—	—
	0·063 BHC		29	—	0	—	28	28	52	73	—	—	—

Summary of replicated tests using 5 insects per pod.

the dish with its upper surface towards the insects, the lid was pressed into place and the rest of the leaf was trimmed away. Then the dish was inverted to bring the insects on to the leaf surface. The dishes were kept in an incubator at 30°C. for 48 hours, after which the insects were transferred to a plate at 40°C. to assess the kill.

Results.

Toxicity (contact and fumigant action, if any).

A much quicker knockdown was obtained with BHC than with DDT at the concentrations tested (Table I). First-instar nymphs of *D. theobroma* and *S. singularis* were equally susceptible to BHC. There was little difference in the effectiveness of 0·25 and 0·125 per cent. γ BHC, but both were more effective than 0·063 per cent. γ BHC. Both DDT and BHC were distinctly slower in their action 24 hours after application. The rapid knockdown achieved with BHC one hour after spraying was most striking and made precise recording difficult.

BHC was much more toxic than DDT to fifth-instar nymphs at the concentrations tested (Table II). The tests with aldrin, chlordane and dieldrin suggest

TABLE II.

Toxicity of insecticides to fifth-instar nymphs of *D. theobroma*.
Percentage mortality of nymphs exposed on sprayed pods.

Exposure (hr.)	DDT (technical) 2·5%	1·25%	γ BHC 0·25%	Aldrin 0·25%	Chlordane 0·25%	Dieldrin 0·25%	Control
1	14 (13)	0	100 (15)	97	22	36	—
2	30	3	97 (12)	95	38	76	—
4	43	—	100 (4)	—	—	—	—
18 (overnight)	93	58	—	—	—	—	—
Lesions per pod (means of 8) after 2 hrs.	19	21	7	24	16	18	34

Mean of 8 tests per treatment except where otherwise shown by numbers in brackets.

that, at the concentrations tested, the toxicity of aldrin and BHC was similar, that chlordane and dieldrin were less toxic than BHC, and that dieldrin was more toxic than DDT. The numbers of feeding lesions, which subsequently developed after nymphs were exposed on the pods for two hours, were recorded and are summarised in Table II. These data show that nymphs on treated pods fed less than on the controls and that BHC reduced feeding much more than did the other treatments.

Fumigant action.

The results of tests (Table III) show that BHC had a powerful fumigant action against second- and fifth-instar nymphs of *D. theobroma* and gave almost complete kills after exposures of 3 and 4 hours, respectively. Against adults of *D. theobroma*, the fumigant action of BHC was even more powerful and gave

almost complete kills after an exposure of 30 min. over leaves sprayed with 0·25 and 0·125 per cent. γ BHC but 0·063 per cent. γ BHC was rather less effective. No significant fumigant action of DDT against nymphs or adults was detected even with exposures up to 20 hours. Additional tests confirmed these

TABLE III.

Fumigant action.

Percentage mortality of Mirids exposed over leaves sprayed 1 hour previously.

Second-instar nymphs						Fifth-instar nymphs				
Insecticide		No. of tests	Exposure (hr.) ½	1½	3	20	Insecticide	No. of tests	Exposure (hr.) 2	4	20
DDT (technical)	2·5%	9	0	0	0	3	DDT (technical) 2·5%	6	0	0	2
γ BHC	0·25%	9	0	60	92	—	γ BHC 0·25%	6	50	94	100

Adults

Insecticide		No. of tests	Exposure 10 min.	20 min.	30 min.	40 min.	1 hr.	2 hr.	20 hr.
DDT (technical)	2·5%	10	—	—	0	—	6	—	2
γ BHC	0·25%	5	44	88	98	—	—	—	—
	0·125%	5	36	84	100	—	—	—	—
	0·063%	5	28	40	88	—	—	—	—
Aldrin	0·5%	4	30	—	90	—	80	—	—
	0·25%	8	—	—	90	70	—	—	—
Chlordane	0·25%	6	—	—	—	—	11	—	55
Dieldrin	0·25%	6	—	—	—	—	0	—	39

results for adults and nymphs of *S. singularis*. Aldrin had a fumigant action approaching that of BHC; chlordane and dieldrin had a significant but less powerful action. When doing the fumigation tests with BHC, most of the adults were already affected after 30 minutes' exposure and all were dead 24 hours later at 0·125 per cent. whereas with aldrin the adults appeared unaffected after 30 minutes' exposure but showed 90 per cent. mortality after 24 hours at both concentrations used.

Additional tests showed that the fumigant action of BHC and aldrin was transient. Leaves previously sprayed with 0·25 per cent. γ BHC and 0·5 per cent. aldrin were used, and adults were exposed for 20 hours. Kills with BHC were 100 per cent. after two days, 47 per cent. after four days and 10 per cent. after seven days. Kills with aldrin were 35 per cent. after two days and 10 per cent. after four days and seven days.

Residual toxicity.

Tests with Mirids.—DDT was still effective against first-instar nymphs after 21 days but the residual toxicity of BHC fell considerably between the 6th and 14th days (Table IV). The experiment was repeated, and seven days after

TABLE IV.

Residual toxicity of DDT and BHC.

Percentage mortality of first-instar nymphs of *D. theobroma* exposed for 1 hour on sprayed pods.

Interval (days) after spraying	DDT (technical) 2·5%	γ BHC 0·25%
1	100	100
6	68	92
14	69	31
21	62	20
28	5th-instar nymphs exposed for 24 and 48 hours	
	24 hr. 5	0
	48 hr. 6	0

Mean of 8 tests per treatment.

spraying, the percentage kill was 50 with DDT and 33 with BHC. Tests after 14 days were valueless because so many control insects died.

After 28 days, DDT and BHC were ineffective against fifth-instar nymphs (Table IV). The experiment was repeated, and the residual toxicity of DDT, BHC, aldrin and dieldrin to fifth-instar nymphs was tested after 6–8 and 14–16 days. The results (Table V) show that, with the possible exception of BHC, the insecticides were ineffective after 6–8 days. BHC reduced feeding greatly although only 24 per cent. of the nymphs died during the test period of 14–16 days.

TABLE V.

Residual toxicity of DDT, BHC, aldrin and dieldrin.

Percentage mortality and feeding intensity of fifth-instar nymphs of *D. theobroma* exposed on sprayed pods.

Interval (days) after spraying	Exposure (hr.)		DDT (technical) 2·5%	γ BHC 0·25%	Aldrin 0·25%	Dieldrin 0·25%	Control
6–8	4	% kill	5	0	—	—	—
	18	% kill	15	27	15	13	—
		lesions/pod	89	20	59	55	54
14–16	18	% kill	6	24	14	12	—
		lesions/pod	86	21	71	59	73

Mean of 8 tests per treatment.

A few tests, carried out to compare 0·25 per cent. aldrin and 0·25 per cent. γ BHC, suggested that, after three weeks, the treatments were still effective against first-instar nymphs when exposed for 20 hours but not when exposed for one hour and that they were ineffective against fifth-instar nymphs exposed for 20 hours, though BHC reduced feeding.

Tests with adults of T. castaneum.—The residual toxicity of DDT fell steadily; for 1·25 and 2·5 per cent. technical DDT it was negligible after three and six weeks, respectively, but 5 per cent. persisted longer (Table VI). There was evidence that DDT persisted longer on heavily shaded than on unshaded plots.

TABLE VI.

Residual toxicity of technical DDT.

Percentage mortality of adults of *T. castaneum* exposed for 48 hours.

Date of spraying		12.vii.55	13.vii.55			20.viii.55				8.x.55	20.x.55
Concentration		2·5%	5%	2·5%	1·25%	2·5%		1·25%		2·5%	2·5%
Shade		Normal	Normal	Normal	Normal	Heavy	None	Heavy	None	Normal	Normal
Interval after spraying (days)	1	88	100	83	51	87	80	50	55	80	78
	7	73	—	—	—	—	—	—	—	—	—
	14	38	86	36	19	55	47	20	3	46	29
	21	36	73	29	3	—	—	—	—	20	28
	28	33	74	21	6	48	17	11	2	16	—
	42	2	28	4	0	11	3	6	1	2	4

Mean of 8 tests per treatment.

Similar tests with γ BHC showed that this insecticide, at concentrations between 2 and 0·25 per cent., consistently had little or no residual toxicity after 2–3 days.

Discussion.

BHC is highly toxic to Mirids, acts quickly and has a powerful fumigant action, whereas DDT has a relatively low toxicity, acts slowly and has no fumigant action. These results have an important bearing on the practical problem of controlling Mirids on cacao. When suitable machinery became available, low-volume spraying (mist blowing) with 5–10 gallons of diluted spray per acre was adopted for treating mature cacao. Clearly, complete cover could not be achieved and consequently an insecticide with a powerful fumigant action and high contact toxicity such as BHC is likely to be more effective than an insecticide with only contact toxicity, like DDT.

In a series of field trials, carried out jointly by the Ghana Department of Agriculture and Messrs. Plant Protection Ltd. while the present work was in progress, it was reported that, when BHC was used, Mirids and Mirid damage were reduced in adjoining untreated plots but not when DDT was used, and it was suggested that BHC had a repellent action (Anon., 1957*b*). As a repellent would be likely to affect only the adults (the nymphs are relatively sedentary) it seems more probable that the observed effect reflected the fumigant power of BHC (Anon., 1956). The results of these, and later trials, confirmed the superiority of BHC over DDT for Mirid control on mature cacao (Hammond, 1957).

The powerful fumigant action of BHC suggested that effective Mirid control might be achieved by fogging. There is very little air movement in the bush and it was thought that the insecticidal fog might be retained in the canopy long enough for it to be effective. Preliminary trials at W.A.C.R.I. by Taylor (1957) gave promising results. Mirid adults and nymphs placed in the canopy in wire cages at distances up to 60 ft. from the path of the fog generator were all dead after 20 and 36 hours, respectively. A 10½-acre plot of mature cacao was treated by traversing it at 50-ft. intervals. This took 55 minutes and 1 oz. γ BHC per

acre was used. After 24 hours, 95 per cent. of the adults and 43 per cent. of the nymphs used as test insects were dead. With low-volume spraying, the recommended rate of application is 4 oz. γ BHC per acre and treatment is much slower (10–15 acres per day).

The evidence, from tests with *T. castaneum* and fifth-instar nymphs of *D. theobroma*, that the residual toxicity of DDT falls quite rapidly, supports the view that the length of time that sprayed cacao remains free from damage soon depends upon the rate of reinfestation and not on the persistence of the insecticide. This applies particularly to low-volume spraying, with which the insecticidal deposit per unit area is very much less than that used in the persistence tests. However, when young cacao is spray-painted with 2·5 per cent. technical DDT, the areas treated are more nearly sprayed to drip point. The tests with first-instar nymphs (Table IV) indicate that DDT would then persist long enough to be toxic to over 60 per cent. of nymphs hatching from eggs laid beforehand, the incubation period being about 17 days (see p. 13). (DDT is considered to have no ovicidal action and BHC little or none (Anon., 1956).) Better coverage can be achieved when treating young cacao and this also would favour the use of DDT at that stage.

Tests with *T. castaneum* showed that BHC had very little residual effect, but tests with Mirids showed that there was a residual toxic effect for at least several days and a pronounced effect on feeding for at least a fortnight. The use of different test insects and sprayed surfaces may partly account for these differences, but it is also possible that the different results are due to a local systemic action. If BHC is taken up by the pod tissue to any extent it may continue to affect sap-feeding insects like Mirids after the surface deposit, to which *T. castaneum* was exposed, had become ineffective. The short-lived fumigant action of BHC in tests with Mirids is consistent with the short-lived surface action in the tests with *T. castaneum*. However, in assessing the value of persistence the characteristics of Mirid attack must be considered. Young vegetative growth on which Mirids feed and lay their eggs is produced whenever the tree flushes; so, after a time, a persistent insecticide becomes ineffective because the parts it protects are no longer the parts which are infested.

Of the other insecticides tested, aldrin appeared to be the most promising alternative to BHC. Preliminary field trials by Taylor (1958) confirmed this conclusion.

Summary.

Laboratory and field tests were made to investigate the toxicity, mode of action and persistence of technical DDT and γ BHC when applied to cacao in Ghana to control the Mirids, *Distantiella theobroma* (Dist.) and *Sahlbergella singularis* Hagl. The insecticides were tested at concentrations previously used in field trials. *D. theobroma*, *S. singularis* and *Tribolium castaneum* (Hbst.) were used as test insects. Preliminary tests with aldrin, chlordane and dieldrin were also made.

Cacao pods were sprayed to drip point with the test insecticides and the deposit was allowed to dry. Mirid nymphs were placed on the pods and the rate of knockdown and the mortality after exposure for a test period was recorded. These tests showed that BHC had a higher toxicity and acted much more quickly than DDT. BHC greatly reduced feeding.

Fumigant action was tested by spraying cacao leaves to drip point with the test insecticides, allowing the deposit to dry, and then exposing Mirid nymphs and adults over discs cut from the leaves. BHC had a powerful but transient fumigant action; adults, fifth- and second-instar nymphs were killed after, respectively, ½, 4 and 3 hours' exposure at 28–30°C. over leaves treated with 0·25 per

cent. γ BHC. No fumigant effect was observed after prolonged exposure over leaves treated with 2·5 per cent. technical DDT.

Persistence was studied by treating cacao leaves and pods growing under natural conditions and then testing the residual deposit at intervals. Tests with *T. castaneum* showed that when leaves were sprayed to drip point the residual toxicity of 1·25 and 2·5 per cent. technical DDT fell steadily and was negligible after an interval of three and six weeks, respectively; that of 0·25–2 per cent. γ BHC was negligible after 2–3 days. Corresponding tests with Mirids on pods were less consistent but suggested that 2·5 per cent. technical DDT was still effective against first-instar nymphs after three weeks; 0·25 per cent. γ BHC had a residual toxic effect for at least several days and depressed feeding greatly for at least a fortnight. It is suggested that BHC may have a local systemic action which persists after the surface deposit becomes ineffective.

Of the other insecticides tested, aldrin had a high toxicity and powerful fumigant action and appeared to be the most promising alternative to BHC.

It was concluded that BHC would be more effective than DDT when treating mature cacao because, in addition to its higher toxicity and quicker action, its fumigant action would compensate for incomplete coverage by low-volume spraying.

Acknowledgements.

My best thanks are due to D. J. Taylor who introduced me to the Mirid problem and to members of the Ghana Department of Agriculture for discussion and opportunities for field experience. Several assistants helped me, in particular M. E. La, D. J. Mordjifa and M. Semabia.

References.

Anon. (1949). West African Cacao Research Institute. Annual Report, 1947–48.

Anon. (1951). *Ibid.*, 1949–50.

Anon. (1953). *Ibid.*, 1950–51.

Anon. (1954). *Ibid.*, 1953–54.

Anon. (1955). West African Cocoa Research Institute. Annual Report, 1954–55.

Anon. (1956). West African Cocoa Research Institute. Quarterly Report no. 41, January–March 1956.

Anon. (1957*a*). West African Cocoa Research Institute. Annual Report, 1955–56.

Anon. (1957*b*). Annual Report of the Department of Agriculture (Ghana) for the year 1954–55. Accra.

Cotterell, G. S. (1926). Preliminary study of the life-history and habits of *Sahlbergella singularis* Hagl. and *Sahlbergella theobroma* Dist.—*Bull. Dep. Agric. Gold Cst* no. 3, 26 pp.

Cotterell, G. S. (1943). Entomology.—*Rep. cent. Cocoa Res. Sta. Tafo 1938–42* pp. 46–55.

Crowdy, S. H. (1947). Observations on the pathogenicity of *Calonectria rigidiuscula* (Berk. & Br.) Sacc. on *Theobroma cacao* L.—*Ann. appl. Biol.* **34** pp. 45–59.

Dudgeon, G. C. (1910). Notes on two West African Hemiptera injurious to cocoa.—*Bull. ent. Res.* **1** pp. 59–61.

GOODCHILD, A. J. P (1952). A study of the digestive system of the West African cacao Capsid bugs (Hemiptera, Miridae).—Proc. zool. Soc. Lond. **122** pp. 543–572.

HAMMOND, P. S. (1957). Capsid control on mature cocoa.—*New Gold Cst Fmr* **1** pp. 109–115.

RAW, F. (1959). An insectary method for rearing cacao Mirids, *Distantiella theobroma* (Dist.) and *Sahlbergella singularis* Hagl.—*Bull. ent. Res.* **50** pp. 11–12.

TAYLOR, D. J. (1954). A summary of the results of Capsid research in the Gold Coast.—*Tech. Bull. W. Afr. Cacao Res. Inst.* no. 1, 20 pp.

TAYLOR, D. J. (1957). Efficiency of fog application of BHC.—*Rep. W. Afr. Cocoa Res. Inst. 1955–56* pp. 50–51.

TAYLOR, D. J. (1958). Pest control research at W.A.C.R.I.—*Rep. Cocoa Conf. 1957* pp. 125–128.

© Commonwealth Agricultural Bureaux, 1959.

THE ACTION OF THE SYSTEMIC INSECTICIDE FLUOROACETAMIDE ON CERTAIN APHIDS AND ON *PIERIS BRASSICAE* (L.).

By W. A. L. David and B. O. C. Gardiner

Agricultural Research Council, Unit of Insect Physiology, Cambridge.

It has been shown in earlier papers that sodium fluoroacetate (which is widely used as a rodenticide under the name Compound 1080) is very effective as a systemic insecticide against *Aphis fabae* Scop. whether applied to the roots or to the leaves of the broad-bean plant (David, 1950; David & Gardiner, 1951). It is also very much more toxic to larvae of *Pieris brassicae* (L.) than schradan and somewhat more toxic than demeton (David & Gardiner, 1953, 1954*b*). Unfortunately it cannot be recommended as an insecticide since it is a very dangerous poison, being both highly toxic and rapid in action.

The high level of effectiveness of sodium fluoroacetate as a systemic insecticide has led to the investigation of related compounds, and it has now been shown that fluoroacetanilide and fluoroacetamide are active insecticides (Phillips, 1955, 1957; Harrison, 1956). Fluoroacetamide has received most attention. It is claimed to be considerably less hazardous to handle than sodium fluoroacetate because it is less toxic and also because it acts more slowly (Gitter, Blank & Bergmann, 1953*b*; Phillips & Worden, 1956). Furthermore, following the suggestion of Peters (1954) it has been found that, in rats, acetamide acts as an effective antidote to fluoroacetamide if administered sufficiently rapidly and it delays the onset of symptoms if administered simultaneously (Phillips & Worden, 1956, 1957). In this way too it may be expected to be safer than sodium fluoroacetate to which acetamide does not act as an antidote though it does give some protection if administered several hours beforehand (Gitter, Blank & Bergmann, 1953*a*).

The toxic action of fluoroacetate has been shown by Peters & others (1953) to be due to the synthesis from it *in vivo* of fluorocitrate, which blocks the tricarboxylic acid cycle. The difference between the two compounds can probably be explained by the suggestion that fluoroacetamide is converted to fluorocitrate *in vivo* much more slowly than sodium fluoroacetate. This idea is supported by the observation that acetamide is only slowly converted to acetic acid *in vivo* (Anker & Raper, 1948). From the limited number of observations made there is no evidence that fluoroacetamide is a cumulative poison (Phillips & Worden, 1956).

It therefore appears from what has been said that fluoroacetamide is likely to be appreciably safer for use as an insecticide than sodium fluoracetate. The present paper considers its insecticidal properties in comparison with sodium fluoroacetate and the well tried systemic insecticide schradan.

Methods and Equipment.

All the tests with aphids have been carried out using the methods and equipment already described (David & Gardiner, 1951, 1954*a*). The following species were used: *Aphis fabae* on broad beans (*Vicia faba*) and *Brevicoryne brassicae* (L.) and *Myzus persicae* (Sulz.) on young cabbage plants.

The aphid population was assessed as previously described (David & Gardiner, 1954*a*) but since the Tables cannot be understood without the key to the terms used, their explanation is repeated here.

The aphid population on the plants was not counted, instead it was assessed as follows:

Normal: Thriving colonies with aphids of all stages settled and feeding, or a few adults surrounded by young.
Declining: Colonies with few aphids, some dead aphids on and around the plant, and the remaining aphids often moving restlessly about.
Isolated: Only scattered individual aphids and no young. Many dead aphids around the plant.
None: No aphids on the plant.

Besides the immediate toxic effect, the persistence of the material was also investigated. Attempts were made to reinfest treated plants 2, 5 and 10 days after the beginning of the experiment. The toxic condition shown by the plant at the time of the reinfestation was then described as:

High (H): All insects killed within 2 days of reinfestation.
Medium (M): All insects killed within 5 days of reinfestation.
Low (L): Some deaths, but an incomplete kill in 5 days.
Nil (N): No effect observed.
In making these assessments the following symbols were also used:
$>$: Indicates that the condition referred to was passed before an observation was made or between observations.
$<$: Indicates that the condition referred to was not reached in the course of the test.

Control groups or colonies of insects were kept in all experiments and where no reference is made to these, they remained normal.

Phytotoxicity was assessed as follows:

Normal (N): Plant not different from control.
Trace (T): Slight marginal scorch or wilt or scattered spotting.
Moderate (M): Large areas of the leaves scorched or pronounced wilting.
High (H): Plant almost entirely killed, though the small leaves around the growing point may still be green.
Dead (D): Plant dead.

Potted plants may show various symptoms of ill health not attributable to treatment with the insecticides. In evaluating leaf damage the plants were therefore carefully compared with two or three untreated plants.

The larvae of *Pieris brassicae* were reared according to the methods described by David & Gardiner (1952) and David (1957). The insecticidal tests were carried out as described by David & Gardiner (1953, 1954*b*).

Materials.

The fluoroacetamide was supplied by Messrs. Associated Fumigators Ltd. through Dr. M. A. Phillips and Associates, and was reported to have the following analysis—fluoroacetamide 95 per cent., water 4·5 per cent., chloroacetamide 0·5 per cent. The other two materials used for comparison were sodium fluoroacetate and schradan (bis(dimethylamino)phosphonous anhydride). Both of these were highly purified.

Fluoroacetamide is a white crystalline solid, it melts at 110°C. and is very readily soluble in water. There is general agreement that when administered orally or subcutaneously to rats the LD 50 is 15 mg./kg. and the LD 100 between 19–20 mg./kg. (Gitter, Blank & Bergmann, 1953*b*; Bentley, 1956; Phillips & Worden, 1956, 1957). Sodium fluoroacetate is more toxic, and the corresponding values are, LD 50 1–2 mg./kg. and LD 100 5–8 mg./kg. (Ward & Spencer, 1947; Chenoweth, 1949; Bentley, 1956; Phillips & Worden, 1956).

Experiments with *Aphis fabae* on Broad Bean.

Dipping tests.

Broad-bean plants were cut down to leave one pair of leaves, infested with aphids and dipped 24 hours later in the solutions to which 0·1 per cent. Teepol had been added as a wetter. The solutions were at 20°C. From the results given in Table I it can be seen that sodium fluoroacetate and fluoroacetamide were about equally effective against the aphid and that both were considerably superior to schradan.

TABLE I.

Dipping tests with fluoroacetamide, sodium fluoroacetate and schradan, of broad-bean plants infested with *Aphis fabae*.

Material	Concentration (% w/v)	Aphids First day on which : Declining	Isolated	None
Fluoroacetamide ..	0·005	>	>	1
	0·001	1	2	4
	0·0005	1	<	<
Sodium fluoroacetate ..	0·005	>	>	1
	0·001	1	2	3
	0·0005	2	<	<
Schradan	0·05 (v/v)	>	1	2
	0·005	<	<	<

The solutions contained 0·1 per cent. Teepol as a wetter. All results on fluoroacetamide are the average of six tests, those on the other two compounds are based on four tests. Aphid colonies on the control plants remained normal.

Systemic action following applications made to the roots.

Plants growing in sand or soil.—In these tests, 20 cc. of the insecticide solutions were poured on to the 500 g. of moist sand or 400 g. of compost in which the plants were growing when they were about 6 in. tall. Afterwards the plants were given about 20 cc. water daily to keep them moist but an excess which would have drained away was avoided.

The results obtained are given in Table II. It can be seen that fluoroacetamide was as effective as sodium fluoroacetate as a systemic insecticide, that it was about equally persistent in the plants and probably a little more phytotoxic. Both compounds were superior to schradan. Like the other two insecticides, fluoroacetamide was taken up more readily from sand than from soil.

Some biological tests have been carried out to determine how long fluoroacetamide and sodium fluoroacetate persist in soil. This subject is of importance not only in connection with the possible use of these compounds as insecticides but also where they are used as rat poisons since the baits may contaminate the soil.

"Whalehide" pots, 5 in. in diameter, were filled with moist compost and watered with 0·1 and 0·01 per cent. solutions of the two compounds at the rate of 20 cc. per 400 g. compost. The pots were then stored in a cool greenhouse and after intervals of 1, 2, 4 and 6 weeks the compost was used to fill 3-in. diameter pots in which infested bean plants, 2 in. high, which had been germinated in sand, were then planted. The effect on the aphids was noted in the usual way.

When the infested bean plants were transferred to the compost one week after it had been treated with 0·01 per cent. solutions of fluoroacetamide or sodium fluoroacetate the aphids were all killed by the seventh day; when planted a week later the aphids were not affected.

TABLE II.

The insecticide watered on to sand or soil in which the broad-bean plants, infested with *Aphis fabae*, were growing.

Material	Dose (1) applied (mg.)	Aphids First day on which : Declining	Isolated	None	Toxic condition of plants Level/day	Phytotoxic effect Level/day
				Sand		
Fluoroacetamide ..	20	>	1	2	H/5	H/5
	2	1	>	2	H/5 ; M/10	T/10
	0·2	1	2	4	M/5 ; N/10	N/10
	0·02	4	5	<	N/5	N/10
Sodium fluoroacetate	2	1	2	3	H/5 ; L/10	N/10
	0·2	3	5	6	L/2 ; N/10	N/10
	0·02	<	<	<	N/10	N/10
Schradan	20	3	5	7	L/5	N/10
	2	<	<	<	N/2	N/10
				Soil		
Fluoroacetamide ..	20	1	>	2	H/5	T/10
	2	1	2	3	H/5	T/10
	0·2	2	7	<	L/2	N/10
	0·02	<	<	<	N/2	N/10
Sodium fluoroacetate	2	>	2	4	H/5	N/10
	0·2	<	<	<	N/2	N/10
Schradan	50	2	5	6	H/5	T/10
	20	<	<	<	N/2	N/10

All results with fluoroacetamide are the average of at least six tests, those on the other two compounds are based on four tests. Aphid colonies on the control plants remained normal.

(1) Mg. of the actual compound applied in 20 cc. solution.

In similar experiments with 0·1 per cent. solutions, both insecticides persisted in the compost long enough to free plants of aphids when they were transferred to it after 4 weeks, in 3 or 4 days and after 6 weeks, in 5 or 6 days.

The low doses of both compounds necessary for the systemic treatment of the plants against aphids were soon decomposed in the soil but heavier dosages gave more persistent residues.

Plants in culture solutions.—The bean plants used in these experiments were grown in sand and transferred to the test solutions for a period of five days when 4–8 inches high, at which time they weighed 8–15 g., after which they were maintained in a culture solution. It can be seen from Table III that, when absorbed from solutions, fluoroacetamide was about equal to sodium fluoroacetate as a systemic insecticide and both were approximately 100 times more effective than schradan.

Concentration of fluoroacetamide in bean plants necessary to kill the aphids.

Known doses of the insecticides were administered to the plants by the technique of the cut tap-root (David & Gardiner, 1951). It can be seen from

TABLE III.

Effect on aphids established on broad-bean plants placed in solutions for five days then transferred to culture solution.

Material	Concentration (% w/v)	Average volume absorbed on day 5 (cc.)	Aphids First day on which : Declining	Isolated	None	Toxic condition of plant Level/day	Phytotoxic effect Level/day
Fluoroacetamide ..	0·005	36	1	>	2	H/10	H/10
	0·001	46	1	2	3	H/10	T/10
	0·0005	53	1	2	3	H/10	N/10
	0·0001	44	2	3	5	M/10	N/10
Sodium fluoroacetate	0·0005	39	1	2	3	H/10	N/10
	0·0001	40	2	3	4	N/5 ; N/10	N/10
Schradan	0·01 (v/v)	15–30	3	4	6	H/5 ; M/10	N/10
		15–30	4	6	<	M/5 ; N/10	N/10

The results with fluoroacetamide and fluoroacetate are based on four determinations run simultaneously. The results with the schradan are from David & Gardiner (1951). Aphid colonies on the control plants remained normal.

Table IV that the minimum dose of fluoroacetamide required to free the plants of aphids was between 0·9 and 0·09 mg./kg. of fresh plant tissue and that the value for sodium fluoroacetate was below 0·7 mg./kg. fresh plant tissue. These doses may be compared with the dose of approximately 50 mg./kg. fresh plant tissue found to be necessary with schradan and 1 mg./kg. fresh plant tissue with demeton (David & Gardiner, 1951, 1954*a*).

TABLE IV.

Effect on aphids established on broad-bean plants given 1 cc. each of the toxic solutions by the cut tap-roots.

Material	Conc. (% w/v)	Calculated dose given to plant (1) (mg./kg.)	Aphids First day on which : Declining	Isolated	None	Toxic condition of plants Level/day
Fluoroacetamide ..	0·05	28·5	6 hrs.	>	1	H/10
	0·01	6·4	>	>	1	H/10
	0·005	3·8	>	1	2	M/5
	0·001	0·9	1	2	3	L/5 ; N/10
	0·0001	0·09	3	4	<	L/2 ; N/5
Sodium fluoroacetate ..	0·001	0·7	>	1	2	M/5 ; N/10

All results are the average of four or more determinations.

(1) The dose given is expressed in mg. of insecticide dosed per kg. of fresh plant tissue.

Systemic action following application to the leaves of broad bean.

Translocation upwards, from older to younger leaves.—In these experiments the insecticide solutions were applied to the older leaves of bean plants, weighing about 25 g. at the beginning of the experiment, with a camel-hair brush and the younger untreated leaves were screened from them by a lamp glass ventilated with a slow stream of air (David & Gardiner, 1953).

TABLE V.

Effect on aphids established on the younger leaves of broad-bean plants of brushing the older leaves with 0·5 cc. of solutions of fluoroacetamide and sodium fluoroacetate for comparison.

Material	Conc. (% w/v)	Calc. dose given to plant (mg.)	Average number of leaf-pairs treated	Aphids First day on which : Declining	Isolated	None	Toxic condition of plants Level/day
Fluoroacetamide ..	0·10	0·50	4·5	>	1	2	M/5
	0·05	0·25	4·4	>	1	3	L/5
	0·01	0·05	4·0	1	2	4	N/5
Sodium fluoroacetate	0·05	0·25	4·0	>	1	3	H/5 ; L/10
	0·01	0·05	4·0	1	3	5	L/5 ; N/10

The solutions contained 0·1 per cent. Teepol as a wetter. All results on fluoroacetamide are the average of six tests, those on sodium fluoroacetate are based on four tests. Aphid colonies on control plants remained normal.

The results given in Table V show that fluoroacetamide applied to the lower leaves of bean plants was translocated rapidly to the younger leaves in sufficient quantities to kill aphids. In this respect it compared favourably with sodium

TABLE VI.

Effect on aphids established on the two oldest leaf pairs of broad-bean plants of brushing the younger leaves with solutions of fluoroacetamide and sodium fluoroacetate for comparison.

Material	Conc. (% w/v)	Calc. dose given to plant (mg.)	Leaves treated	Aphids First day on which : Declining	Isolated	None	Toxic condition of plants Level/day
Fluoroacetamide ..	0·5	2·5	All top	1	2	3	L/5
			3	1	>	2	M/5 ; N/10
	0·1	1·0	4	>	2	3	N/5
			4	2	>	3	N/5
Sodium fluoroacetate	0·5	2·5	All top	1	2	3	M/5 ; N/10
			3	1	>	3	H/5 ; N/10
	0·1	1·0	4	1	2	3	M/5
			4	>	1	4	L/5
Schradan	0·1 (v/v)	1·0	4	<	—	—	N/0
			4	<	—	—	N/0

The plants were treated with 0·5 cc. or 1·0 cc. and all solutions contained 0·1 per cent. Teepol as a wetter. All results are the average of two tests. Control aphids remained normal.

fluoroacetate and would be much superior to schradan (David & Gardiner, 1951). Although no directly comparative tests were made it is almost certainly also considerably superior to demeton (Systox) (David & Gardiner, 1954*a*). The treated leaves were damaged only by the 0·10 per cent. fluoroacetamide solution.

Translocation downwards, from younger to older leaves.—It is well known that material applied to the leaves is more readily translocated upwards to the younger leaves than downwards to the older leaves under most circumstances. Some experiments carried out with fluoroacetamide and sodium fluoroacetate showed that both moved from younger to older leaves in sufficient quantities to kill aphids while schradan did not. With the two fluorine compounds at 0·5 per cent. the treated leaves were significantly scorched 4–6 days after treatment. There is evidence in both upward and downward translocation experiments that plants treated with sodium fluoroacetate remained toxic to aphids for five days or so longer than those treated with fluoroacetamide (Table VI).

Experiments with *Brevicoryne brassicae* and *Myzus persicae* on Cabbage Plants.

In these experiments young cabbage plants about 6 in. high growing in compost in the usual $3\frac{1}{2}$-in. diameter "whalehide" pots were used as hosts for the aphids.

Dipping tests.

Only *B. brassicae* was used for these tests as *M. persicae* drops off the plant too readily. As before, the solutions contained 0·1 per cent. Teepol as a wetter and were at 20°C. when the plants were dipped. The results obtained are given in Table VII. Again fluoroacetamide and sodium fluoroacetate were equally effective and both were considerably superior to schradan.

TABLE VII.

The effect on *B. brassicae* of dipping cabbage plants in the three insecticides.

Material	Concentration (% w/v)	Aphids First day on which : Declining	Isolated	None
Fluoroacetamide	0·005	>	>	1
	0·001	1	2	3
	0·0005	2	5	<
Sodium fluoroacetate ..	0·005	>	>	1
	0·001	1	2	3
	0·0005	2	3	<
Schradan	0·50 (v/v)	>	>	1
	0·10	>	>	1
	0·05	3	<	<

Each result is the average of four tests. Aphid colonies on the controls remained normal.

Systemic action following application to the roots.

Twenty ml. of the solutions were watered on to the soil in the "whalehide" pots in which the cabbages were growing and the plants were maintained in the usual way (Table VIII).

From Table VIII it can be seen that the two fluorine compounds were definitely more effective than schradan against both these aphids as they were against *A. fabae*. But whereas the fluorine compounds were about equally efficient

against *A. fabae*, fluoroacetamide was more effective than sodium fluoroacetate against *B. brassicae* and *M. persicae*. As with demeton, *M. persicae* was somewhat more resistant than *B. brassicae* to fluoroacetamide and considerably more resistant to sodium fluoroacetate. Symptoms of phytotoxicity were only seen after the highest dosage of fluoroacetamide, when there was slight leaf scorch in one test.

TABLE VIII.

Effect on *B. brassicae* and *M. persicae*, established on cabbage plants, of fluoroacetamide, sodium fluoroacetate and schradan solutions (20 cc.) watered on to the soil in which the cabbage plants were growing.

Material	Dose applied (mg.)	Aphids First day on which : Declining	Isolated	None	Toxic condition of plants Level/day
		Brevicoryne brassicae			
Fluoroacetamide ..	10	>	>	1	H/5 ; L/10
	2	>	>	1	L/5 ; N/10
	1	>	1	2	N/5
	0·2	1	2	3	N/5
Sodium fluoroacetate ..	10	>	>	2	H/5 ; N/10
	2	1	2	3	L/5
	1	1	2	4	N/5
	0·2	<	<	<	N/0
Schradan	100	1	>	2	H/5 ; M/10
	20	2	>	3	M/10
	10	3	4	<	L/2
		Myzus persicae			
Fluoroacetamide ..	20	>	>	1	M/10
	10	>	>	1	M/5 ; L/10
	2	>	>	2	N/5
	1	>	1	2	N/5
	0·2	<	<	<	N/0
Sodium fluoroacetate ..	20	1	2	3	M/5
	10	2	3	4	L/5
	2	<	<	<	N/0
Schradan	100	1	>	2	H/10
	20	3	6	<	L/2
	10	<	<	<	N/0

Each result is the average of six tests.

Systemic action following uptake by the cut petioles.

When known volumes of solutions were fed to the cut leaves of cabbage plants infested with *B. brassicae* it was found that the aphids survived for three days on leaves dosed with either 1 mg. of fluoroacetamide or 1 mg. of sodium fluoroacetate or 10 mg. of schradan per kg. of fresh plant tissue. They were all killed in three days by doses of 5 mg./kg. of the fluorine compounds or 50 mg./kg. of schradan.

Systemic action following application to the leaves.

Clear evidence was obtained that both fluoroacetamide and sodium fluoroacetate or compounds derived from them were translocated from older, outer, leaves of

cabbage plants to the inner, younger, leaves (Table IX). When the concentrations of the solutions were sufficiently high, only one application made to the older leaves was necessary to kill the aphids on the untreated younger leaves and the results were much more consistent than with demeton (David & Gardiner, 1954*a*). Furthermore, only about one-tenth or one-twentieth of the dosage was required and the treated leaves were not damaged as they often were with demeton.

When the kill of the two aphids was compared, *M. persicae* was found to be somewhat more resistant to both insecticides, as it was when applications were made *via* the roots. When the two insecticides were compared, fluoroacetamide was judged to be a little more effective than sodium fluoroacetate. Schradan was less effective than the other insecticides against *B. brassicae* and much less effective against *M. persicae*.

TABLE IX.

Effect on *B. brassicae* and *M. persicae* established on the younger leaves of cabbage plants of brushing four of the older leaves with 0·5 or 0·75 cc. (1) of solutions of fluoroacetamide and of sodium fluoroacetate and schradan for comparison.

Material	Conc. (% w/v)	Calc. dose given to plant (mg.)	Aphids First day on which : Declining	Isolated	None	Toxic condition of plants Level/day
			Brevicoryne brassicae			
Fluoroacetamide ..	0·50	2·5	>	>	1	L/5
	0·10	0·5–0·75	>	1	2	N/5
	0·05	0·25–0·37	>	1	2	N/5
	0·01	0·07	3	4	<	L/0
Sodium fluoroacetate	0·50	2·5	>	1	2	L/5
	0·10	0·5–0·75	>	1	3	L/5
	0·05	0·25–0·37	1	2	4	N/5
	0·01	0·07	2	4	<	L/0
Schradan	0·50 (v/v)	2·5	>	>	1	H/5 ; M/10
	0·10	0·5	1	2	3	M/5 ; N/10
	0·05	0·25	<	<	<	N/0
			Myzus persicae			
Fluoroacetamide ..	0·50	2·5	>	>	1	L/5
	0·10	0·5	>	2	3	N/5
	0·05	0·25	2	4	6	L/0
Sodium fluoroacetate	0·50	2·5	>	>	2	L/5
	0·10	0·5	>	1	2	N/5
	0·05	0·25	3	7	<	L/0
Schradan	0·50 (v/v)	2·5	<	<	<	N/0

The solutions contained 0·1 per cent. Teepol as a wetter. All results are the average of six tests. Aphid colonies on control plants remained normal.

(1) The higher dosages were used on a batch of test plants which were larger than those normally employed.

Experiments with *Pieris brassicae* on Cabbage Plants.

Dipping tests.

With eggs and young larvae.—The leaves of young plants bearing eggs three days old were dipped into solutions of the insecticides, kept at 20°C. with the

usual precautions (David & Gardiner, 1953, 1954*b*). Fluoroacetamide was much more effective than sodium fluoroacetate in preventing the eggs from hatching but the two compounds killed about equal percentages of larvae from those eggs which did hatch (Table X). Schradan at 0·2 per cent. does not prevent the eggs from hatching and does not kill the larvae (David & Gardiner, 1953).

TABLE X.

Cabbage leaves bearing eggs of *P. brassicae* dipped into solutions of fluoroacetamide and sodium fluoroacetate.

Material	Conc. (% w/v)	Percentage of eggs not hatching	Percentage kill (1) of larvae on 5th day after hatching
Fluoroacetamide	0·2	100	—
	0·1	85	70
	0·05	15	80
Sodium fluoroacetate ..	0·2	2	98
	0·1	0	98
	0·05	0	80

All solutions contained 0·1 per cent. Teepol as a wetter.

(1) The surviving larvae were small and retarded in development compared with controls. The results are the average of four tests.

With fourth-instar larvae.—The larvae were covered with the solutions at 20°C. for about half a minute, and then transferred to dry filter paper before being placed on the cabbage leaves. As in the tests with demeton already referred to, the results were variable and sometimes up to 30 per cent. of the control larvae died. The compounds were not very toxic and instead of tabulating the results they may be summarised as follows: Fluoroacetamide or sodium fluoroacetate solutions at 0·5 per cent. with 0·1 per cent. Teepol killed 20–70 per cent. of the larvae in five days while 0·1 per cent. solution killed under 10 per cent. of the larvae in the same time.

With larvae placed on dipped leaves.—Five fourth-instar larvae were allowed to feed on the leaves of young cabbage plants which had been dipped in solutions of the compounds containing 0·1 per cent. Teepol. None of the solution was allowed to run down to the soil. The leaves were dried before the larvae were placed on the plants, which were replaced when all had been eaten.

The compounds were ineffective when applied in this way even at relatively high dosages. Thus with 0·2 per cent. solution no larvae were killed by the second day, and on the fifth day the kills were 30 per cent. for fluoroacetamide and 65 per cent. for sodium fluoroacetate. However, at this concentration and even at 0·05 per cent. the quantity of foliage eaten by day 5 was under 10 per cent., whereas 100 per cent. of the control plants had been eaten. The 0·05 per cent. solutions killed less than 10 per cent. of the larvae.

It seems certain that had the larvae eaten more of the treated plants they would have been killed, and the higher kill with sodium fluoroacetate-treated plants may have been due to rather more of these plants having been eaten, though the difference was not obvious.

Systemic action following application to the roots.

With eggs and young larvae.—Twenty cc. of the solutions were poured on to the soil in the 3½-in. diameter " whalehide " pots in the usual way. The eggs were 24 hours old when the plants were treated.

Neither insecticide prevented hatching at concentrations up to 0·1 per cent. Fluoroacetamide killed all the young larvae when used at 0·05 per cent. but 0·01 per cent. solutions gave very low kills. Sodium fluoroacetate was less effective: it killed all young larvae at 0·10 per cent. but gave no kill when used at 0·05 per cent.

With fourth-instar larvae.—The plants were treated by pouring the solutions on to the soil and the larvae were put on four days later. The results obtained are shown in Table XI. It can be seen that, as for first-instar larvae, fluoroacetamide was more effective than sodium fluoroacetate. The compounds were both much more effective than schradan and demeton but much less effective than paraoxon (David & Gardiner, 1953).

TABLE XI.

Effect on fourth-instar larvae of *P. brassicae*, feeding on cabbage plants, of fluoroacetamide, sodium fluoroacetate or schradan that had been poured on to the soil in which the plants were growing.

Material	Dose applied (mg.) (1)	Percentage of larvae dead by day: 2	5	Percentage of foliage eaten by 5th day
Fluoroacetamide	20	100	—	< 5
	10	100	—	< 5
	5	55	80	< 5
	2	0	5	50
Sodium fluoroacetate ..	20	100	—	< 5
	10	20	40	< 25
	5	10	25	50
	2	0	0	> 75
Schradan	50	0	0	100
Control	—	0	0	100

All results are the average of four determinations.

(1) In mg. of the actual compound contained in 20 cc. of solution.

Systemic action following uptake by the cut petioles.

Known volumes of the solutions were fed to the cut leaves of cabbage plants from small specimen tubes as previously described (David & Gardiner, 1953, 1954*b*). For this purpose fairly hard leaves are required as soft, quickly grown leaves wilt more readily. The larvae were allowed to feed on the leaves under petri dishes ventilated with saturated air. After 24 hours the larvae and the remainder of each leaf were weighed.

It can be seen from Table XII that under these conditions larvae on control, untreated plants gained weight and when they were starved lost weight, while the leaves also lost weight due to evaporation. When feeding on leaves treated with the lowest concentration of the poisons the larvae gained weight considerably and it must be assumed that the dose was not significantly toxic in either case. Weight gain was very limited at 20 mg. of either poison per kg. of fresh plant tissue, and very little leaf was eaten. At higher dosages the larvae lost about as much weight as starving larvae.

It can be said, therefore, that at dosages of poison of 20 mg. per kg. of fresh plant tissue and above both fluoroacetamide and sodium fluoroacetate prevent

growth of the larvae. This result may be compared with the corresponding value for paraoxon of 6 mg./kg., for demeton of 140–310 mg./kg. (David & Gardiner, 1954*b*) and schradan of over 2,900 mg./kg. (David & Gardiner, 1953).

TABLE XII.

The dosage of fluoroacetamide and sodium fluoroacetate fed to cabbage leaves, and the effect of the treated leaves on larvae of *P. brassicae*.

Material	Conc. of solution fed to leaves (% w/v)	Conc. of material in leaves (mg./kg.)(1)	Average wt. of larvae used (g.)	Wt. lost by leaf (%)	Wt. lost or gained by larva (%)
Fluoroacetamide ..	0·05	238	0·104	18·6	— 15·2
	0·01	53	0·110	20·1	— 1·2
	0·005	20	0·160	20·5	+ 1·9
	0·001	3·5	0·101	29·4	+105·5
Sodium fluoroacetate	0·05	242	0·119	19·1	— 20·4
	0·01	49	0·100	19·1	— 7·4
	0·005	20	0·153	21·4	+ 6·7
	0·001	5	0·117	37·7	+ 54·6
Controls	—	—	0·108	44·4	+ 89·9
	—	—	No larva	20·3	—
	—	—	0·121	No leaf	— 20·4

All results are the average of eight determinations.
(1) Calculated on weight of fresh leaf tissue.

Systemic action following application to the leaves.

Penetration through the leaves.—It has been found that eight applications of 0·5 per cent. solutions of the insecticides applied over two days to the upper or under surfaces of the leaves did not prevent eggs of *P. brassicae* laid on the opposite surface from hatching normally but the young larvae were killed. With paraoxon, 0·001 per cent. solutions applied in the same way prevented hatching (David & Gardiner, 1953).

Translocation from older to younger leaves.—When 1 cc. of 0·1 and 0·5 per cent. solutions of fluoroacetamide and sodium fluoroacetate were brushed on to the four outer leaves of cabbage plants, weighing about 12 g., two fourth-instar larvae feeding on the untreated younger leaves remained apparently normal and moulted to the fifth instar.

Summary.

Fluoroacetamide has been tested as a systemic insecticide against *Aphis fabae* Scop., *Brevicoryne brassicae* (L.), *Myzus persicae* (Sulz.) and the eggs and larvae of *Pieris brassicae* (L.). In the majority of tests, sodium fluoroacetate and schradan have been included for comparison.

In dipping tests against *A. fabae* and *B. brassicae*, fluoroacetamide was as effective as sodium fluoroacetate and both were much superior to schradan. Fluoroacetamide was superior to sodium fluoroacetate in preventing eggs of *P. brassicae* from hatching and they were about equally effective against the newly hatched larvae. Schradan was already known to have little action on the eggs or larvae. Neither of the fluorine compounds was very effective against fourth-instar larvae.

When watered on to the soil, fluoroacetamide was more readily absorbed from sand than from soil—like other systemic insecticides. Against *A. fabae* it was as immediately effective and persistent as sodium fluoroacetate and both were superior to schradan. To *B. brassicae* and *M. persicae*, fluoroacetamide was more toxic than sodium fluoroacetate, *M. persicae* being somewhat more resistant to fluoroacetamide and much more resistant to sodium fluoroacetate. Slight phytotoxic effects were observed only at the higher dosages.

When poured on to the soil around the roots of cabbage plants, neither compound prevented eggs of *P. brassicae* from hatching, but the young larvae were killed when they began feeding. Applied systemically in this way, fluoroacetamide was more toxic than sodium fluoroacetate to these young larvae and to fourth-instar larvae.

When John Innes potting compost was treated with solutions of the fluorine compounds and stored in the greenhouse it was found that both compounds were quickly decomposed at the dosages necessary for systemic action against aphids, but higher dosages were much more persistent.

In solution, given systemically *via* the roots to broad beans, fluoroacetamide and sodium fluoroacetate were about equally effective and both were more toxic than schradan to *A. fabae*. Fluoroacetamide was the more toxic of the fluorine compounds.

The technique of the cut tap-root showed that the approximate LD 100 for *A. fabae* on broad beans was: fluoroacetamide between 0·09 and 0·9 mg./kg.; sodium fluoroacetate 0·7 mg./kg.; schradan 50 mg./kg. When taken up by cabbage leaves through the cut petioles, 5 mg. of the fluorine compounds or 50 mg. of schradan per kg. of fresh plant tissue killed all *B. brassicae* in 2–3 days.

Leaves of cabbage treated in the same way with fluoroacetamide were fed to larvae of *P. brassicae*. It was found that the growth of the larvae feeding on the leaves was not prevented until a dose of about 20 mg./kg. was reached. The same value was found for sodium fluoroacetate. For schradan, more than 2,900 mg./kg. were required.

Finally, with applications made to the older leaves against all these species of aphids feeding on the younger leaves of their host-plants, fluoroacetamide was equally effective or slightly superior to sodium fluoroacetate as a systemic insecticide. Schradan was nearly as effective against *B. brassicae* but much less effective against the other two aphids.

Even after repeated applications none of the compounds acting systemically prevented eggs of *P. brassicae* from hatching or had a detectable toxic action on fourth-instar larvae.

References.

ANKER, H. S. & RAPER, R. (1948). On the metabolic fate of pyruvamide and acetamide.—*J. biol. Chem.* **176** pp. 1353–1357.

BENTLEY, E. W. (1956). Recent progress in the control of rats in sewers.—*Sanitarian, Lond.* **64** pp. 392–396.

CHENOWETH, M. B. (1949). Monofluoracetic acid and related compounds.—*J. Pharmacol.* (*Rev.*) **1** pp. 383–424.

DAVID, W. A. L. (1950). Sodium fluoroacetate as a systemic and contact insecticide.—*Nature, Lond.* **165** pp. 493–494.

DAVID, W. A. L. (1957). Breeding *Pieris brassicae* L. and *Apanteles glomeratus* L. as experimental insects.—*Z. PflKrankh.* **64** pp. 572–577.

DAVID, W. A. L. & GARDINER, B. O. C. (1951). Investigations on the systemic insecticidal action of sodium fluoroacetate and of three phosphorus compounds on *Aphis fabae* Scop.—*Ann. appl. Biol.* **38** pp. 91–110.

DAVID, W. A. L. & GARDINER, B. O. C. (1952). Laboratory breeding of *Pieris brassicae* L. and *Apanteles glomeratus* L.—*Proc. R. ent. Soc. Lond.* (A) **27** pp. 54–56.

DAVID, W. A. L. & GARDINER, B. O. C. (1953). The systemic insecticidal action of sodium fluoroacetate and of three phosphorus compounds on the eggs and larvae of *Pieris brassicae* L.—*Ann. appl. Biol.* **40** pp. 403–417.

DAVID, W. A. L. & GARDINER, B. O. C. (1954*a*). The action of the systemic insecticide Systox, on aphids.—*Bull. ent. Res.* **45** pp. 683–692.

DAVID, W. A. L. & GARDINER, B. O. C. (1954*b*). The action of the systemic insecticide Systox, on *Pieris brassicae* (L.) and *Phaedon cochleariae* (F.).—*Bull. ent. Res.* **45** pp. 693–702.

GITTER, S., BLANK, I. & BERGMANN, E. D. (1953*a*). Studies on organic fluorine compounds. I. The influence of acetamide on fluoroacetate poisoning.—*Proc. Acad. Sci. Amst.* (C) **56** pp. 423–426.

GITTER, S., BLANK, I. & BERGMANN, E. D. (1953*b*). Studies on organic fluorine compounds. II. Toxicology of higher alkyl fluoroacetates.—*Proc. Acad. Sci. Amst.* (C) **56** pp. 427–430.

HARRISON, I. R. (1956). Control of bulb scale mite in narcissus.—*Plant Path.* **5** pp. 127–129.

PETERS, Sir R. (1954). Biochemical light upon an ancient poison: a lethal synthesis.—*Endeavour* **13** pp. 147–154.

PETERS, R. A., WAKELIN, R. W., BUFFA, P. & THOMAS, L. C. (1953). Biochemistry of fluoroacetate poisoning. The isolation and some properties of the fluorotricarboxylic acid inhibitor of citrate metabolism.—*Proc. roy. Soc.* (B) **140** pp. 497–507.

PHILLIPS, M. A. (1955). The fluoroacetate series of pesticides.—*World Crops* **7** pp. 480–482.

PHILLIPS, M. A. (1957). Plant for the manufacture of fluoroacetamide.—*Chem. Age, Lond.* **77** pp. 673–674.

PHILLIPS, M. A. & WORDEN, A. N. (1956). Toxicity of fluoroacetamide.—*Lancet*, Oct. 6th, p. 731.

PHILLIPS, M. A. & WORDEN, A. N. (1957). The mammalian oral toxicity of fluoroacetamide.—*J. Sci. Fd Agric.* **8** pp. 653–657.

WARD, J. C. & SPENCER, D. A. (1947). Notes on the pharmacology of sodium fluoroacetate—compound 1080.—*J. Amer. pharm. Ass.* (Sci. Edn.) **36** pp. 59–62.

© Commonwealth Agricultural Bureaux, 1959.

BIOLOGY AND ECOLOGY OF THE GARDEN CHAFER, *PHYLLOPERTHA HORTICOLA* (L.).

V.—THE FLIGHT SEASON: SEX PROPORTIONS.

By A. Milne *

School of Agriculture, King's College (University of Durham), Newcastle upon Tyne.

It has been shown in an earlier paper (Milne, 1958) that the flight season of *Phyllopertha horticola* (L.) in the English Lake District usually lasts 3–4 weeks and is divisible into two roughly equal and half-overlapping phases of mass activity. In Phase 1 the beetles swarm close over the grass sward from which they emerged but Phase 1 gradually gives way to Phase 2 in which the beetles now swarm closely on the bracken, hedges and trees surrounding the pasture. During the latter half of Phase 2, swarming is wholly confined to bracken if that is present. Throughout Phase 2 there are always some individuals (a minority called "bee-liners") suddenly quitting the swarm to fly almost bullet-like to points in the home or a more distant pasture where they immediately burrow into the soil. Activity invariably occurs somewhere between 8 a.m. and 4 p.m. G.M.T. For about the first week, all beetles disappear into the sward at the end of the day's activity. After that, a growing fraction of the active population spends the night resting in full view on the sward, bracken, hedges and trees. Few beetles rest on the sward after Phase 2 starts and none after Phase 1 ends. If bracken is present, all beetles resting above ground are confined to it in the latter half of Phase 2.

Sexing of Beetles in the Field.

Rittershaus (1927) describes minutely the external differences of the male and female adult but gives no hint as to the handiest characters for the diagnosis of living individuals in the field. Viewed dorsally, as is usual, the sexes look the same to the naked eye.

At the outset we tried examining the first tarsal claws with a pocket lens (male claw being thicker than female) but the beetles proved to be too restless. Soon we found, however, that sex could be determined quite simply with the naked eye and without handling the beetle at all. The pronotum of the male is covered with long dark hairs and that of the female with short light hairs. Little or no difference is apparent unless one looks *across* the surface of the pronotum. The male hairs are then seen as a longer dark fuzz while the female hairs are clearly distinguishable as a shorter golden fuzz. The difference can be seen up to a distance of about 15 inches. Pronotal hairs tend to become worn down or worn off with age but not to the extent of preventing diagnosis.

In the end, however, we could infallibly distinguish a female at a distance of 3 or 4 feet by her general "demeanour". This is a complex quality, difficult to describe in detail, but compounded of small differences from the male in movements and general appearance.

---

* Agricultural Research Council Unit of Insect Physiology.

TABLE I.

Daily percentage of females among beetles active over the grass sward in Phase 1.

Year	% ♀♀ in pupal stage	Duration of Phase 1 (days)	Periods of Phase 1		
			I	II	III
1949	45·7	26	0 0 Z Z 0 3 Z 0 ? Z 4 0	5 Z Z 15 Z 24 **24**	? 15 ? Z 11 ? 5
1950	34·6	21	0 4 4 1 3 5 Z	7 19 **3** 2	7 21 ? Z Z Z 15 10 16 ?
1951	44·3	23	0 0 Z Z 0 5 Z 2 8 Z	2 **14** Z 26 25	16 33 25 Z Z 41 ? ?
1952	46·9	20	0 0 2 2 3 0 Z 10	**8** 4 8 7 12	Z 25 41 56 Z 17 8
Total days			37	21	32
Z days			10	4	8
? days			1	0	7
Observation days			26	17	17
Range in % ♀♀			0–10	2–26	5–56
Mean % ♀♀ per obs. day			2·2	12·1	21·3

Data from counts in 10–20 random square yards of sward at peak density each day (20–450 beetles per day depending on density). "Z" indicates days when, due to weather, there was very little or, more usually, no activity. "?" indicates days when beetles were active but no observations were made. Percentages are arranged in sequence, left to right, from the first day of Phase 1.

The percentages in heavy type in Period II represent the day in each year when the number of beetles reached its peak.

Sex Proportions in Phase 1.

The proportion of females over the sward reaches a maximum at the daily peak of beetle numbers. Sex counts were therefore made at peak time. Table I gives the day-to-day data for Phase 1 in 1949–1952. Since the phase length varies, it has been divided into three comparable periods, based on beetle density (not female percentage), for each year. Period II runs from the day that beetle density first exceeds two-thirds of the phase maximum until the day before it drops below two-thirds. In Period I, density rises to, and in Period III falls from, two-thirds of the maximum density on the sward. Sex ratios in pupal stage as given in Milne (1956).

In laboratory experiments, females emerged into activity 1–2 days behind males (Milne, 1956). In nature only males were seen over the sward on the first day of each flight season. Females first appeared as follows:—

Year	Day of season
1948	3
1949	6
1950	2
1951	6
1952	3

The lateness in 1949 and 1951 was due to weather preventing activity after the second day (see Table I); no activity was possible on the third and fourth days and very little on the fifth. Non-appearance on the fifth day is probably explained by the fact that females, even when ready to emerge, are less easily activated than males. A single typical instance quoted from field notes of Phase 1 illustrates this: " At first in the morning it was dull with a cool breeze. Gradually it got warmer and the overcast sky got brighter until at 9.45 the first beetle issued from the ground. It was a male. Then the sun began to peep through in little blinks. With each blink more and more beetles came up. All were males until 9.53 when the first female of the day came upon the surface ". Males are quicker than females in their response to light and warmth.

In 1948, sex counts were made on six days only, but these suggested that the percentage of females increased as the Phase progressed. As shown in Table I, this was confirmed by comprehensive data in the seasons following. Despite large samples there is considerable irregular variation, but broadly the female/male ratio rises throughout Phase 1 except for a tendency to fall in the last few days. In two seasons only (1951 & 1952), and then only for a day or two, did females attain the proportion promised in the pupal stage. Generally, for most and sometimes the whole of Phase 1, the proportion of females is far below the possible.

Experiments throwing some Light on Sex Proportions in Phase 1.

Sex ratio phenomena in Phase 1, and indeed mass aspects of the flight season in general, are the result partly of differences in timing of male and female primary emergence into activity upon the sward (Milne, 1956, p. 38) and partly of differences in male and female behaviour afterwards.

In April 1950 all the larvae (actually prepupae) in 7 random square yards of sward in U.H.H.F. (the study field) (see Milne, 1958) were collected. This resulted in a total of 417 uninjured specimens being taken. Each of these individuals was set up in a 5 × 1 in. open-ended glass tube the bottom of which was plugged with plaster of paris. The larva was placed on its side upon this plug, the latter being first covered with a $\frac{1}{4}$-in. layer of fine soil (max. particle diam. 2 mm.). The tube was now filled with the same soil to a depth of 2 in..

the soil being topped with a $\frac{1}{8}$-in. layer of tamped sawdust. A perforated cork, $\frac{1}{4}$ in. thick, closed the upper end of the tube so that about $1\frac{1}{2}$ in. of clear air-space was left above the sawdust. The tubes were then sunk, 3 in. apart, in undisturbed turf at the centre of the collecting area. Each tube stood in a tight-fitting hole (taken out with an auger) so that the sawdust layer was on a level with the thin mat of decaying grasses, etc., on the soil surface at the bottom of the short *Agrostis-Festuca* sward. The orange-yellow sawdust simulated the true mat and the surrounding grasses came close around and over the projecting part of the tube.

From the beginning of the flight season, a close watch was kept throughout the activity period of each day for any beetle breaking through the sawdust and moving around, trying to climb the sides of its tube. As soon as this primary emergence into activity happened, that particular tube was withdrawn, the hole filled up with soil, and the sex of the beetle noted. Only 105 of the original 417 individuals survived to this stage. The numbers of males and females making their primary emergence each day are shown in Table II. Unfortunately no

TABLE II.

Individual primary emergence into adult activity from a random sample of 417 larvae kept in the field under conditions closely simulating the natural in 1950 (see text).

Date	Total individuals	
June 1950 ..	Males	Females
Up to 2 ..	0	0
3 ..	1	0
4 ..	1	1
5 ..	8	1
6 ..	10	4
7 ..	21	13
8 ..	12	10
9 ..	2	6
10 ..	6	1
11 ..	2	4
12 ..	1	0
13 ..	0	0
14 ..	0	0
15 ..	0	1
After 15 ..	0	0

record was kept of the exact time of day at which individuals emerged, but one gained the impression that almost all came up during the first half of the daily activity period. Male emergence began on 3rd June, female on 4th June; 98·4 per cent. of males and 97·6 per cent. of females, *i.e.*, practically all, had made their primary emergence by 11th June. In the surrounding free population from which the experimental sample came, males first appeared on the sward surface on 2nd June, females on 3rd June; and density of active beetles, irrespective of sex, reached its maximum on 11th June.

It will be noted that the first beetles to emerge in the experiment were a day later than in nature. This was probably due to sampling, but it could have arisen from the slight insulating effect of the glass whereby the rise and fall of soil temperature in the tube would be retarded and curtailed in range. Therefore tubes were dispensed with when the experiment was repeated in 1951.

At the beginning of March 1951, two similar squares of sward, each 2 ft. by 2 ft. and near to one another, were marked out. The turf was pared off to a

depth of 1 in., and the soil removed right down to the hard "pan". A 4-in. wall of thin galvanised iron sheet was fitted round each cavity so that it projected 1 in. above the surrounding soil surface. After extracting *all* the chafer larvae in it, the soil was put back inside the walls and the turf replaced. By the end of April the turf had re-rooted firmly and was flourishing. In each square, 196 four-inch wooden dowels ($\frac{1}{2}$-in. diam.) were now inserted vertically, $1\frac{1}{2}$ in. apart, so that their bottom ends were 2 in. deep in the soil. On 25th May all the pupae were collected from 14 random square yards of sward round about but not too near the experimental squares. The uninjured individuals (pupae are rather fragile) totalled 198 males and 157 females, or 44·2 per cent. females, which was very close to the actual sex proportion in the 1951 pupal population (mean

TABLE III.

Individual primary emergence into adult activity from a random sample of 355 pupae kept in the field under practically natural conditions in 1951 (see text).

Date June 1951	Time of day (hr.)	Individual		Total		Daily activity period in free population surrounding the experiment, and sun conditions
		♂♂	♀♀	♂♂	♀♀	
8	1002	1	0	1	0	1005 to 1135 hr. Bright sun all day
12	1518	1	0	1	0	1445 to 1525 hr. Sunny during 1445 to 1525 only
13	1005	3	0	–	–	1015 to 1045 hr. Sunny during 1015 to 1045 only
	1020	3	1	–	–	
	1023	2	0	–	–	
	1025	7	1	–	–	
	1030	5	0	20	2	
14	1455	1	0	1	0	1450 to 1457 hr. Sunny during 1450 to 1457 only
15	0900	3	0	–	–	0830 to 1345 hr. Bright sun all day
	0910	9	1	–	–	
	0915	3	0	–	–	
	0930	5	1	–	–	
	0940	7	2	–	–	
	0945	1	2	–	–	
	0955	3	0	–	–	
	1005	3	0	–	–	
	1010	0	2	–	–	
	1020	0	4	–	–	
	1105	0	1	–	–	
	1110	1	0	35	13	
18	1015	1	2	–	–	0910 to 1630 hr. Bright sun all day
	1025	0	1	–	–	
	1150	0	4	–	–	
	1350	0	1	1	8	
19	1015	0	1	–	–	0845 to 1615 hr. Bright sun all day
	1025	0	2	–	–	
	1045	0	1	–	–	
	1100	2	0	–	–	
	1110	0	1	–	–	
	1130	1	3	3	8	

In the experiment there were no primary emergences before 8th June or after 19th June, nor on the omitted dates between.

44·3 per cent. females, Table I). Males were introduced into one square, females into the other (the reason for separating the sexes will emerge in a later paper in this series). The method of introduction was to pull out a dowel, drop one pupa to the bottom of the hole left by the dowel, then fill the hole up—first lightly with fine soil (max. particle diam. 2 mm.) and then, near the top, more tightly with somewhat coarser soil (max. particle diam. 4 mm.). (In fine soil a pupa soon makes " cell " space for itself by arching, as was seen in the glass tube experiment.) The ½-in. diam. tops of the holes were covered in a few days by the expansion of the surrounding " mat " and by overhanging grass blades. Finally a 1-ft. high wooden-framed cage, covered with diaphanous ballet-net gauze and with the top hinged to open, was bolted to the projecting rim of the metal wall in each square.

As in the previous year, a close watch was kept every day throughout the flight season. The watching was continuous for most of the daily period of activity and, when this was not the case, the cages were never left unobserved for more than a very few minutes at a stretch. Each beetle was extracted from its cage as soon as it made its first appearance on the sward. Only 93 of the original 355 individuals survived to emerge into activity. The results are shown in Table III. (Incidentally, the small survival rate (25–26%) in both years, 1950, 1951, suggests that many of the " uninjured " must have had injuries not apparent from superficial inspection at the time of collecting. Prepupae (used in 1950) as well as pupae (used in 1951) are rather fragile.

In the 1951 experiment, male emergence began on 8th June, female on 13th June; and all surviving beetles had made their primary emergence by 19th June. In the surrounding free population from which the experimental sample came, males and females first appeared on the sward surface at the same dates precisely, *i.e.*, males on 8th June and females on 13th June (the 5-day difference being for weather reasons, see p. 41); and density of active beetles, irrespective of sex, reached its maximum on 19th June.

In 1951, the exact time of day when each beetle arrived on the sward surface was also noted. Almost all beetles (96%) made their primary emergence in the first half of the daily activity period (see Milne, 1958, p. 692), the remainder (4%) in the third quarter. Males tended to precede females when emerging on the same day, emergence in the first quarter of the activity period being 58 per cent. male.

Tables II and III resulted from conditions so close to the natural that there seems no reason to doubt their reliability as a general picture of primary emergence in the free populations surrounding the field experiments. (In fact these data are confirmed by a study of the reproductive state of females in the free population, as will be shown in a later paper in this series). It is assumed, therefore, that all the beetles in U.H.H.F. had made their primary emergence within a period of 13 days from the beginning of the flight season in 1950 (Table II) and within 12 days in 1951 (Table III), *i.e.*, 8 and 11 days respectively before the end of Phase 1 which lasted 21 and 23 days, respectively, in 1950 and 1951 (Milne, 1958, fig. 1). Moreover, numbers reached their peak on the grass sward only when primary emergence had finished or practically finished. This is what one naturally expects, but it poses the question, why does the proportion of females on the sward increase more or less steadily after the peak of beetle numbers almost to the end of Phase 1? (Table I.) And since the average female makes her primary emergence only 1–2 days behind the average male (0·8 days in 1950, and 2·3 days in 1951, calculated from Tables II and III), there is the prior question: why is the proportion of females so low up to and including the day of peak numbers of beetles, *viz.*, maximum 24 per cent., 1949; 19 per cent., 1950; 14 per cent., 1951; 10 per cent., 1952? The answers will obviously be found in differences of behaviour between males and females.

TABLE IVa.

(See text.)

Year and day	Numbers of males			
	A Accumulated in the field experiments on primary emergence	B Per 10 sq. yd. at the daily peak of activity in nature	Adjusted so that sum equals 100	
			Aa	Bb
1950				
6 June ..	20	97	11·2	13·8
7 June ..	41	182	22·9	25·9
9 June ..	55	194	30·7	27·6
11 June ..	63	230	35·2	32·7
Sum ..	179	703	100·0	100·0
1951				
13 June ..	22	78	15·5	19·9
15 June ..	58	148	40·8	37·8
19 June ..	62	166	43·7	42·3
Sum ..	142	392	100·0	100·0

Since the male's chief function in the flight season is to find, and mate with, females, it is likely that he takes part in activity every day after his primary emergence. This is tested in Table IVa. Column A gives the accumulated numbers of males at certain dates in the field experiments noted in Tables II and III, *i.e.*, the numbers of males that would have been active on those dates if none had been withdrawn and all took part in the activity daily after their primary emergence. Column B gives the actual numbers (peak densities) of males active on those particular dates in the free populations surrounding the experiments. When columns A and B are reduced to comparable proportions as in Aa and Bb, their broad agreement in detail suggests strongly that the male does take part in activity over the sward every day after his primary emergence until Phase 2 begins or Phase 1 ends, depending on how early or late his emergence is.

In Table IVb, column C shows the actual percentage of females among beetles on the sward. This is taken from Table I. Column D shows the possible

TABLE IVb.

(See text.)

Year and day	C Actual females (%)	D Possible females (%)
1950		
6 June	3	23
7 June	5	32
9 June	7	39
11 June	3	39
1951		
13 June	5	8
15 June	2	20
19 June	14	33

TABLE V.

Daily percentage of females among beetles active on bracken in Phase 2.

Year	% ♀♀ in pupal stage	Duration of Phase 2 (days)	Periods of Phase 2	
			I	II
1949	45·7	27	0 Z Z ? Z ? 19 ? 24 ? Z 26 30 ?	47 40 ? 40 43 ? 46 ? 45 Z 50 100
1951	44·3	19	0 Z 8 7 Z 16 22 39	40 50 Z Z 38 50 33 ? Z 50 100

1949 data from counts on twenty random bracken plants (giving 20–350 beetles per day). 1951 data from counts on six fixed sq. yd. of bracken (giving 20–100 beetles per day). Daily percentages arranged in sequence, left to right, from the first day of Phase 2. "Z", "?" and "% females in pupal stage" as in Table I.

percentage, *i.e.*, if the female took part in activity every day after her primary emergence. This is calculated from Tables II and III by accumulating females as well as males (*cf.* column A, Table IVa). Since the actual percentage is obviously very much smaller than the possible, it is clear that, unlike the male, the female is not present on the sward every day after her primary emergence. She will, of course, be absent when underground for oviposition. Detailed examination of her behaviour is left, however, until a later paper in the series.

Sex Proportions in Phase 2.

The sex ratio among beetles taking part in the activity of Phase 2 was examined at the daily peak of density (see p. 41).

The data for one longer and one shorter flight season, 1949 and 1951, on the bracken are shown in Table V. In this case (unlike the arrangement in Table I) the Phase is divided into Periods I and II at the day when the percentage of females first attains to 40 or over. As in Phase 1, there are no females present until after the first day of Phase 2. But the proportion of females rises more quickly and to a higher level than in Phase 1. In the latter half of Phase 2 the proportion is close to the value for the population as pupae except for a steep rise at the end.

TABLE VI.

Proportions of females among beetles active on bracken and on hawthorn in Phase 2.

1949	% Females	
June	Bracken	Hawthorn
8	18·6	45·1
10	23·9	53·2
13	26·1	55·4
15	29·7	68·6

Data from 10 bracken plants (88–176 beetles) and 10 hawthorn branches (41–111) taken at random.

Milne (1958) showed that Phase 2 activity on the hawthorn hedge came to an end much earlier than on the bracken. Another curious difference is revealed in Table VI: the female/male ratio on hawthorn is about twice that on bracken. No explanation can be offered yet.

Roosting at night on bracken, hedges and trees begins about three days before the start of Phase 2 (see Milne, 1958, p. 693). Circumstances on hawthorn are typical for hedges and trees. Females are not usually found there among roosting beetles for the first day or two. Thereafter, the sex ratio amongst those roosting on hawthorn is always more or less the same as at the height of activity during the day. The same is true on bracken until the last week of the flight season when the female/male ratio increases, reaching 100 per cent. on the last night. The latter may be illustrated by data for 1948 and 1951. As an example of the longer season, 1948 data are better than 1949 because sample size was 50 as opposed to 20 beetles per day; the 1951 sample size was 100–200 beetles. Over the last week of the 1948 season, percentages of females amongst beetles roosting on bracken were: 50, —, —, 67, —, 70, 100; and over the last

five days of 1951: 57, —, 65, 80, 100. This increased percentage of females is less evident by day (Table V) because the female population on bracken fluctuates during activity.

Experiment throwing some Light on Sex Proportions in Phase 2.

The rise of the female proportion towards the true (pupal) fraction as Phase 2 progresses into its latter half is obviously a result of mass oviposition nearing completion. The males become confined to the bracken and more and more females join them. Since they emerge 1–2 days after males, one would expect to find only female beetles on the bracken at the last day of the season. But, as shown above, female percentage is rising high above the proportion in the pupal population (around 44% in both years) for upwards of a week before the end. This would be understandable if females lived longer than males. The death-rates (Table VII) in samples of paired beetles taken from the bracken reveal that

TABLE VII.

Deaths in samples of clasped pairs of beetles taken from bracken three weeks after the beginning of the flight season and kept in glass jars containing soil and food.

Days after collecting	1948 12 pairs		1953 16 pairs	
	Males	Females	Males	Females
1 ..	–	–	1	0
2 ..	0	0	2	1
3 ..	–	–	0	0
4 ..	–	–	3	1
5 ..	–	–	0	0
6 ..	1	0	3	1
7 ..	–	–	0	0
8 ..	–	–	2	3
9 ..	2	2	2	0
10 ..	–	–	3	1
11 ..	–	–		2
12 ..	–	–		2
13 ..	5	4		0
14 ..	–	–		0
15 ..	–	–		0
16 ..	1	0		0
17 ..	–	–		0
18 ..	–	–		1
19 ..	–	–		0
20 ..	3	3		1
21 ..		–		0
22 ..		–		1
23 ..		2		1
24 ..		–		1
25 ..		–		
26 ..		–		
27 ..		1		

In 1948 there were 3 pairs per 2 lb. jar; in 1953, all pairs were kept together in a 7 lb. jar. In 1948, the dead were noted at intervals of 3 and 4 days alternately; in 1953, the dead were noted daily.

the female has in fact a longer adult life in nature. In the 1953 experiment the females died on the average not 1–2 days but about 6 days after the males. The 1948 experiment, with a 3- or 4-day observation interval, does not allow precise averaging but the general distribution of male and female deaths bears out the

1953 finding. Greater longevity in the female is not unexpected since it seems to be the rule among animal species (Rockstein & Lieberman, 1958).

If anything, females live only very slightly longer than males (at most half a day on the average) when kept together in a jar from the moment of their emergence (Milne & Laughlin, 1956). But in jar conditions the male expends very little more energy than the female since activity is confined to a little walking with occasional burrowings in the loose soil. However, before being subjected to jar conditions the present experimental beetles (Table VII) had already spent between one and three weeks in nature and there the male is very much more energetic than the female. Every day of his life he is running and flying around feverishly and incessantly whenever conditions permit, while the female walks sedately and does little or no flying until the latter end of her life when she still does not vie with the male in general activity. Thus, even including her burrowings underground for oviposition, the female expends much less physical energy than the male. One is tempted therefore to ascribe the shorter adult life of the male to his wearing himself out sooner.

Sex Proportions and Pairing.

At the beginning of the season, when females are absent or scarce, one occasionally sees a male clasping another male for a short time. However, true pairing, *i.e.*, male clasping female, is to be seen on the grass sward throughout Phase 1 from the day females begin to emerge, and on the bracken (and trees) throughout Phase 2.

When the data for paired beetles in Phase 1 (counts of 44 sq. yd. per day, 1950–52) are grouped on the same pattern as was used in Table I, the following averages are obtained:

	Period		
	I	II	III
(1) % unpaired individuals among females above ground	28·1	36·8	57·9
(2) % males in the population above ground	97·5	89·5	76·4

Thus (1) the proportion of unpaired individuals among females seen at the daily peak of beetle numbers on the grass sward increases as the Phase proceeds until in Period III it is about twice what it was in Period I. This is the outcome partly of (2) the accompanying fall in the relative number of males, which means fewer searching for each female so that she is less readily found. As will be shown in a later paper in this series, it is also partly due to a striking change in the mating behaviour of the female as she ages, which in effect reduces the availability of males more than the actual difference in percentage implies.

Data for Phase 2 were collected only in 1949, and then only on six days (15th–23rd June) in the latter half of the Phase. In this case (counts on 20 bracken plants per day), an average of 82 per cent. of females (74–95%) were paired when the proportion of males in the bracken population was 59 per cent. (56–66%). The higher pairing rate accompanying a lower male/female sex ratio arises from the beetle population being denser (confined to smaller area) on the bracken than on the grass. Males find females more easily on the bracken. The 1949 findings for bracken were confirmed qualitatively in subsequent seasons.

Sex Proportions among Flying Beetles.

The available beetles are never all airborne at any one instant even in the brightest, hottest sunshine. The highest proportion of fliers ever noted was 71 per cent. and usually it was less than 50 per cent.

On the sex ratio among fliers, the data are limited to one year, 1949, and only to the latter halves of each Phase. Observations were made on selected

areas of grass sward and of bracken on days when the sun was obscured for short intervals around peak activity. Total available beetles could then be counted and sexed when all were immobilised by a passing cloud, and a comparison made with the sex ratio among those flying in the sun just before or just after. The immobilised population was sampled by the " square yard " method. Samples of fliers ranged between 20 and 50 beetles caught singly or in twos and threes by random sweeps with a hand net.

TABLE VIII.

The proportion of females among beetles flying.

A	B	C	D	E*
Interval	% females among total available beetles	% females among beetles flying	% females paired among all available females	Theoretical % females among beetles flying
2–15 June 1949 ..	18	7	50	11
15–23 June 1949 ..	41	4	82	23

E* is calculated from columns B and D on the assumption that unpaired males and females are equally willing to fly, *e.g.*, in the period 2nd–15th June, if the active population were 100 beetles, there would be 82 males and 18 females of which 9 males and 9 females would be paired (*i.e.*, unable to fly), leaving 82 beetles in which $\frac{9 \times 100}{82}$ or 11% would be the proportion of females among fliers.

The data are summarised in columns A, B & C of Table VIII. Comparison of columns C and E shows that the actual proportion (C) of females among fliers is smaller than would be expected (E) if males and females were equally inclined to take part in the typical weaving flight. It was unnecessary to examine this point in greater quantitative detail: as indicated earlier, it is perfectly obvious to the observer throughout any season that males are on the whole much more given to flying than females. On the other hand, the longest and fastest single flights are made not by males but by a certain minority of females—the " bee-liners " (see Milne, 1958, and to be dealt with in detail in a later paper in this series).

Deductions, from Mass Phenomena, about the Average Individual.

For a full understanding of the mass aspects of the flight season, some knowledge of individual behaviour and properties is undoubtedly required. At the same time, the mass phenomena themselves furnish, by deduction, parts of this knowledge which would be extremely difficult or impossible to attain by attempts to study individuals in the field. Thus, it would be impracticable to find, by marking and observing selected individuals, (1) whether the male or female participates in activity above ground every day after primary emergence, (2) the average natural length of life and (3) how much of it is spent where. The answer to the first of these problems has already been deduced from mass phenomena (see earlier), and answers to the second and third can likewise be deduced as follows:—

The time elapsing between the end of primary emergence and the end of the flight season gives some idea of the length of individual adult life from first appearance above ground. In 1950 and 1951, primary emergence of population

spanned 13 and 12 days, respectively, and in both years the season lasted 27 days (Milne, 1958, fig. 1). This means that the average female in nature lives about two weeks after primary emergence (*i.e.*, 3 weeks from ecdysis, Milne, 1956), and the average male rather less. Thus, the suggestion of Gray, Peet & Rogerson (1947) was close to the mark. The longest life possible after primary emergence for any individual is between three and four weeks, though obviously this is seldom if ever achieved. Many lives are, of course, shortened by predators, mainly birds.

Again, with primary emergence of a homogeneous population complete in about a fortnight and Phase 1 ending about a week later, and with the rise and fall of numbers coinciding with those two periods, it is clear that the average beetle spends (roughly) the first half of its life in the sward area and the second half in the surrounding bracken, hedges and trees.

Summary.

This part of the study of the garden chafer, *Phyllopertha horticola* (L.), in the English Lake District covers the flight seasons 1948–1952. Annual sex ratios in the population of pupae (just before ecdysis to adult) ranged from 34·6 to 46·9 per cent. females.

The flight season begins with the emergence of some adult males upon the sward. If the weather continues favourable, the earliest females appear on the second or third day of the season. Unsuitable weather delayed the advent of females until the sixth day in two seasons. In a homogeneous population, primary emergence is complete in just under a fortnight, at the end of which time numbers of beetles seen on the grass sward are at their peak. Phase 1, swarming over the sward, continues, with dwindling numbers, for just over a week more (overlapping Phase 2, swarming on the bracken).

The female/male ratio rises throughout Phase 1 except for a tendency to fall in the last day or two. But generally for most and sometimes the whole of Phase 1, the proportion of females above ground is far below the true population ratio. This is partly because population emergence in the female is 1–2 days behind emergence in the male; but much more because after primary emergence the male is fully involved in above-ground activity every day until the beginning of Phase 2 or end of Phase 1 (depending on whether he emerges earlier or later), while the female is not.

In the same way, there are no females present on the bracken until after the first day of Phase 2, but the proportion of females rises more quickly and to a higher level than in Phase 1. By the middle of Phase 2, the proportion is close to the true population ratio. Since males are now confined to the bracken, this means that mass oviposition is more or less complete. During the last week of the season the female proportion rises steeply. This is because females live a few days longer than males besides being 1–2 days behind males in their original emergence.

After primary emergence, the average female lives about a fortnight, the male rather less. Approximately the first half of adult life is spent in the grass sward area, the second half on the surrounding bracken (or hedges or trees).

As Phase 1 proceeds, the pairing rate of females decreases. This is partly because the proportion of males is falling and therefore fewer males are available to search for each female over the grass sward, and partly because of a change in mating behaviour of the female as she ages. On the other hand, pairing rate is at its highest (average 82%, maximum 95%, of available females) in Phase 2 when the proportion of males is at its minimum (actually the true proportion in the population). This is because on the bracken the beetles are confined to a much smaller area than on the grass and therefore males find females more readily.

In flying weather, the proportion of beetles in the air at any moment is at best no more than about 70 per cent.; usually it is less than 50 per cent. On the whole males are very much more given to flying than females.

Acknowledgements.

Thanks are due to Messrs. T. P. McNicol and R. Coggins for help in the field, and to Mr. R. Laughlin for constructive criticism of the manuscript. (The same acknowledgement was inadvertently omitted in Part IV.)

References.

Gray, R. A. H., Peet, W. V. & Rogerson, J. P. (1947). Observations on the chafer grub problem in the Lake District.—*Bull. ent. Res.* **37** pp. 455–468.

Milne, A. (1956). Biology and ecology of the garden chafer, *Phyllopertha horticola* (L.). II. The cycle from egg to adult in the field.—*Bull. ent. Res.* **47** pp. 23–42.

Milne, A. (1958). Biology and ecology of the garden chafer, *Phyllopertha horticola* (L.). IV. The flight season: introduction, and general aspects.—*Bull. ent. Res.* **49** pp. 685–699.

Milne, A. & Laughlin, R. (1956). Biology and ecology of the garden chafer, *Phyllopertha horticola* (L.). I. The adult and egg production.—*Bull. ent. Res.* **47** pp. 7–22.

Rittershaus, K. (1927). Studien zur Morphologie und Biologie von *Phyllopertha horticola* L. und *Anomala aenea* Geer (Coleopt.).—*Z. Morph. Ökol. Tiere* **8** pp. 271–408.

Rockstein, M. & Lieberman, H. M. (1958). Survival curves for male and female house-flies (*Musca domestica* L.).—*Nature, Lond.* **181** pp. 787–788.

© Commonwealth Agricultural Bureaux, 1959.

THE DISTRIBUTION OF SHOOT-FLY LARVAE (DIPTERA, ACALYPTERAE) WITHIN PASTURE GRASSES AND CEREALS IN ENGLAND.[1]

By I. W. B. Nye[2]

Commonwealth Institute of Entomology.

Although host records for individual species of Diptera, the larvae of which feed in the shoots of pasture grasses and cereals in Britain, have long been available, it has not previously been possible to carry out detailed quantitative studies on these shoot flies in a mixed sward owing to the difficulty in identifying the larvae and the impracticability of separating the intermixed grasses and subsequent breeding out of the adult insects. In a recent paper (Nye, 1958) an effort has been made to provide comparative illustrations, descriptions and brief notes on the bionomics of the larvae of the acalypterate and calypterate Diptera which constitute the majority of the species living in and killing the shoots of cereals and wild host grasses in Britain. As a complementary study to this, pure grass clumps and a mixed sward of a permanent pasture have been sampled to determine what species were present and how and in what numbers they were distributed within the grasses. This was possible since the species under consideration overwinter from October to March as final-instar larvae within grass stems. A series of trial samples throughout these months showed that the population remained dormant, and only suffered a slight reduction up to the end of March. Even if death had occurred, the corpse within the stem was sufficiently well preserved for identification.

Totals of the combined numbers of larvae of all species considered are given, as they represent an index of infestation which is roughly comparative. This mixing of different species into a total is to some extent justified since none of them appears to be highly aggregated, and it is very uncommon to find more than one larva per stem in these grasses although this does not always apply to the thicker, more succulent stems of cereals.

Distribution of Larvae in individual Grasses.

The pure clumps of grass were obtained from the Imperial College Field Station, Silwood Park, Berkshire, and their area estimated. Every stem was dissected and any larva found was identified. The results obtained are given in Table I with each column adjusted so that it represents one square yard, though in fact, except for *Dactylis glomerata*, the area of each grass actually examined exceeded this unit. Some of the grasses, in particular *Agrostis tenuis*, came from areas in which the individual clumps were surrounded by bare soil, and it was observed that under those circumstances the stems were more highly infested per unit area of grass than were those of the same grass within a sward. This may be due to many factors, such as differential growth and tillering of the grass in the different habitats or to the populations of gravid females being distributed more or less evenly over a large area and hence a greater egg density occurring when the ovipositional sites available (*i.e.*, stems) were scarce. Whether isolated

[1] Rewritten from part of a thesis approved for the degree of Ph.D., University of London, in 1955.

[2] Formerly at Imperial College of Science and Technology, University of London.

TABLE I.

Larval population per square yard in pure grass clumps at Silwood Park.

	February–March 1955					April 1954	Jan. 1955
	Lolium perenne	*Holcus lanatus*	*Agrostis tenuis*	*Anthoxanthum odoratum*	*Arrhenatherum elatius*	*Dactylis glomerata*	
CHLOROPIDAE							
Oscinella frit (L.)	115	32	54	12	0	0	0
Oscinella vastator (Curt.)	14	0	0	0	0	0	0
Oscinella nitidissima (Mg.)	0	0	243	3	0	0	0
O. frit form from *Anthoxanthum*	0	0	0	48	0	0	0
O. frit form from *Arrhenatherum*	0	0	0	0	175	0	0
Oscinella albiseta (Mg.)	0	0	0	0	0	16	32
Cetema spp.	50	1	27	6	1	0	0
Meromyza spp.	14	0	9	0	0	146	65
Conioscinella frontella Fall.	0	8	0	0	0	0	0
Conioscinella mimula Collin	0	0	0	39	0	0	0
OPOMYZIDAE							
Opomyza germinationis (L.)	65	3	279	3	0	0	0
Opomyza petrei Mesn.	14	141	0	102	0	0	0
Geomyza tripunctata Fall.	209	0	0	0	1	0	0
Geomyza combinata (L.)	0	123	0	0	4	0	0
ANTHOMYZIDAE							
Stiphrosoma sabulosum (Hal.)	0	0	0	3	15	0	0
PALLOPTERIDAE							
Palloptera quinquemaculata (Macq.)	0	0	0	0	111	0	0
EPHYDRIDAE							
Hydrellia incana (Stenh.)	7	2	0	6	0	0	0
Total larvae per sq. yd.	488	310	612	222	307	162	97
CECIDOMYIIDAE	0	0	0	0	0	243	65

clumps of one grass among other grasses act in a similar manner to those insects which are host specific upon it must yet be determined.

In Table I, the values give not only an estimate of the populations of larvae present in each grass but also indicate the grasses that were acceptable as an oviposition site and that were subsequently suitable as a host for the larvae. The low values of an insect species, when the general population level of the same insect in other grasses is high, are likely to be due to migration of the larvae from an adjacent grass. This is borne out by the relative absence of low values from *Agrostis tenuis* which was in isolated clumps as compared with *Anthoxanthum odoratum* and *Arrhenatherum elatius* which were in clumps surrounded by other grasses. These low values, although tending to make host preferences in this and the following Table less clear cut, do however show that the dietary requirements of many of the larvae are satisfied by several of the grasses and indicate that it is not these larval requirements but the ovipositional behaviour of the gravid females that primarily determines the discontinuous distribution between grasses.

Table I is also a good guide to the host specificity of the insects. *Oscinella frit* (L.), the serious pest of oats, is present in many grasses but not in *D. glomerata*. In *Arrhenatherum elatius* and *Anthoxanthum odoratum*, forms close to *frit* are found but more work is required before they can be established as distinct species. On the other hand the easily separated *O. albiseta* (Mg.) is very limited in its distribution and is found only in *D. glomerata*. The *Cetema* spp. could not be separated in the larval stages and are either *neglecta* Tonn. or *elongata* Mg. This was also the case with *Meromyza saltatrix* (L.) and *M. variegata* Mg., though it has since been observed that *M. variegata* is probably confined to *D. glomerata*.

Distribution of Larvae in a mixed Sward.

Having studied the distribution of species within pure clumps it is of interest to see whether this holds in a closely admixed sward of a permanent pasture. That chosen was the Silwood Main Field of 17 acres directly opposite the Entrance Hall of the Field Station. It was seeded about 1949 with *Lolium perenne* but was subsequently invaded by the dominant natural grasses, *Holcus lanatus* and *Agrostis tenuis*, and to a lesser extent by *Anthoxanthum odoratum*. Each year a spring hay cut had been taken and the ley was then grazed by cattle for the rest of the season.

The field was sampled in three areas named with reference to the Entrance Hall as the Near End, the Far End, at a distance of 300 yards, and the Centre, which was equidistant from these two areas but 100 yards to the south of the line joining them. Samples were taken at each of the three areas in the winter of 1953/54 and at the Near End and Centre in the winter of 1954/55. On each occasion four pairs of cores were taken along a transect at 10-yard intervals with the aid of a sharpened length of steel pipe which had a cross sectional area of 20 sq. in.

Each core was examined and a visual assessment made of the percentage coverage of its constituents. Each shoot was then identified, recorded as living or dead (as an index of the ovipositional sites available and the general condition of the grasses) and any larva found was kept in a solid watch-glass containing tap water together with other larvae from the same grass and core until identified.

The samples and cores were taken in accordance with statistical design with a view to subsequent analysis of results but since each core was found to contain from three to five different grasses in varying proportions and there were about eight species of larvae associated with them a special sampling technique would have had to be developed. This would have had to ensure both random sampling

TABLE II.

Larval population per square yard in a mixed sward, Silwood Main Field, Near End on 26th November 1953.

	Winter 1953/54						
	Total	*Lolium perenne*	*Holcus lanatus*	*Agrostis tenuis*	*Anthoxanthum odoratum*	*Poa pratensis*	Dicotyledons and bare
Coverage per sq. yd. ..	100%	45%	19%	16%	1%	1%	20%
Total no. of stems ..	—	7140	2730	4140	218	770	—
No. of dead stems ..	—	875	607	607	32	121	—
Oscinella frit	252	122	81	41	0	8	—
Oscinella vastator	146	146	0	0	0	0	—
Oscinella nitidissima ..	32	0	16	16	0	0	—
Cetema spp.	24	0	0	16	0	8	—
Opomyza germinationis ..	97	24	0	65	0	8	—
Opomyza petrei	73	0	41	8	24	0	—
Geomyza combinata ..	32	0	32	0	0	0	—
Stiphrosoma sabulosum ..	8	0	8	0	0	0	—
Total larvae ..	664 per sq. yd.	292	178	146	24	24	—

for estimation of the distribution of the grasses coupled with biased sampling to provide sufficient data on the less common grasses. Although biased sampling might satisfy statistical criteria, the results could not be of general application until further ecological knowledge has been obtained. For example, the potential larval population at any one time depends, among other things, on the state of growth of the grass, the population of gravid females and the weather conditions at the time of oviposition, a matter of weeks or months previously, and these factors vary for each species of grass and each species of insect in each habitat. For these reasons and for ease of presentation the eight 20-square-inch samples have been bulked and the 160 square inches actually examined have been multiplied by a factor of 8·1 to bring the unit to one square yard, which is more easily visualised. Although this helps to some extent in the comparisons between samples and areas, the Table must to a great extent speak for itself, for although the total area considered is one square yard the proportions of the constituents of the sward and hence the larvae associated with them vary. To bring the values for each grass species in the sample to a standard unit area would in turn produce difficulties with the less common grasses.

The larval population per square yard at the Near End of Main Field during the winter 1953/54 is shown in Table II and, in spite of the very close admixture of the grasses, the host preferences of the insects are broadly maintained. The further samples taken from the field, the results of which are available in the original thesis, are also proportionally reasonably consistent with the figures in Table II except that the populations in the following year are reduced by over half, almost certainly due to the bad summer of 1954.

Relative Abundance of Larvae.

At the Grassland Research Institute, Hurley, a series of 1/5th-acre plots seeded with strains of different grass species in 1951 were maintained on the top of a chalk downland. These plots provided an opportunity in 1954 of sampling a large number of grasses growing in almost pure stands adjacent to one another. It is not possible to quote here all the population figures obtained, so, in Table III, all the samples from Hurley and Silwood have been bulked and each species of larva found in a grass is expressed as a percentage of the total number of larvae found in that grass. Local aggregations should thus be minimised and the columns provide a rough idea of the relative abundance of each species within a grass while the rows indicate the degree of host specificity of each insect. Any species of larva whose abundance was less than 5 per cent. of the total for that grass has been omitted from the Table since its presence in the grass was probably due to larval migration rather than the ovipositional preferences of the adult.

The last row of Table III shows the mean number of tillers per square yard for each grass under consideration, calculated from all the samples taken at Silwood and Hurley during 1953–55. When compared with comparable average figures for winter wheat at 8½-inch row spacing (570 tillers per square yard), and spring oats at 6-inch row spacing (660 tillers per square yard) it is immediately apparent that a population of larvae that would have produced even 100 per cent. infestation of cereals would be quite normal in the adjacent headlands and pastures and would pass unnoticed.

Vertical Migration of Larvae.

Quite apart from oviposition directly upon or close to grasses and cereals by shoot flies, a larva may find its way into a plant other than that in which it started, through migration. Horizontal migration from tiller to tiller can take place and has already been discussed. The term, vertical migration, is here

TABLE III.

Percentage distribution of larvae found in each of 16 pasture grasses.

	Lolium perenne	*Lolium multiflorum*	*Holcus lanatus*	*Agrostis tenuis*	*Agrostis stolonifera*	*Anthoxanthum odoratum*	*Arrhenatherum elatius*	*Dactylis glomerata*	*Festuca pratensis*	*Festuca rubra*	*Poa annua*	*Poa pratensis*	*Poa trivialis*	*Phleum pratense*	*Alopecurus pratensis*	*Phalaris tuberosa*
Oscinella frit	30	20	10	20	5	—	—	—	10	80	70	20	10	—	5	—
Oscinella vastator	30	30	—	—	—	—	—	—	30	—	—	—	—	80	—	—
Oscinella nitidissima	—	—	—	20	—	—	—	—	—	—	—	—	—	—	—	—
O. frit form from *Anthoxanthum*	—	—	—	—	—	15	—	—	—	—	—	—	—	—	40	—
O. frit form from *Arrhenatherum*	—	—	—	—	—	—	60	—	—	—	—	—	—	—	—	—
Oscinella albiseta	—	—	—	—	—	—	—	40	—	—	—	—	—	—	—	—
Cetema spp.	10	—	—	20	20	5	—	—	10	—	—	—	20	—	5	80
Meromyza spp.	10	10	—	—	—	—	—	60	—	10	—	40	—	—	—	—
Conioscinella frontella ..	—	—	5	—	—	—	—	—	—	—	—	—	—	—	—	—
Conioscinella mimula ..	—	—	—	—	—	20	—	—	—	—	—	—	—	—	—	—
Opomyza germinationis ..	10	—	5	40	75	—	—	—	40	10	30	40	70	20	40	20
Opomyza petrei	—	—	40	—	—	60	—	—	—	—	—	—	—	—	—	—
Geomyza tripunctata	10	40	—	—	—	—	—	—	10	—	—	—	—	—	10	—
Geomyza combinata	—	—	30	—	—	—	—	—	—	—	—	—	—	—	—	—
Stiphrosoma sabulosum ..	—	—	—	—	—	—	5	—	—	—	—	—	—	—	—	—
Palloptera quinquemaculata	—	—	—	—	—	—	35	—	—	—	—	—	—	—	—	—
Hydrellia incana	—	—	10	—	—	—	—	—	—	—	—	—	—	—	—	—
Mean no. of tillers per sq. yd.	12300	8900	11400	16100	13600	11300	8100	5400	8800	25000	23000	13000	21000	7000	9000	4900

applied to larval movement from buried grass to new growth on the surface. Petherbridge (1917) reports cases of winter wheat sown after a ryegrass (*Lolium*) ley being attacked by " frit fly " larvae and he followed this up (1921) by a field experiment showing that ploughing in during July and August followed by a short two- or three-month fallow prevents subsequent " frit " attack (owing to the lack of oviposition sites for these flies) but increases the likelihood of an infestation by wheat bulb fly (*Leptohylemyia coarctata* (Fall.)), which oviposits on bare soil during August. In another plot, *Lolium* was ploughed in during early November and drilled a fortnight later. Frit-fly larvae were found in the buried grass up till early April. They were first noticed in the wheat tillers in February and were more numerous in March.

Cunliffe (1921) buried naked larvae of *O. frit* up to depths of 9 inches and obtained up to 50 per cent. emergence of flies, but this did not necessarily demonstrate the migration of larvae since similar experiments showed that the fly could emerge from puparia buried 9 inches deep in loose moist soil. Miles (1921) records a case of winter wheat where 27 per cent. of the tillers were attacked, but in an experiment in which larvae in wheat seedlings were buried at a depth of 4 inches in loam, healthy wheat and oat seedlings planted above were not attacked and no flies emerged.

Since these observations, reports have continually been made of crop damage due to " frit larvae " following a ley. The inverted commas have been used as, in the past, " frit larvae " have been frequently blamed for damage due to a complex of species. As an example, in March 1954 a sample was received from Rugby of winter wheat which had been drilled on the 26th October 1953 on top of a rye-grass and red clover ley which had been ploughed in during the first week of October. By March 1954 the wheat was observed to be attacked and several acres were sufficiently severely thinned to require re-seeding. When the sample of wheat was examined in the same month, out of 23 larvae found there were 2 of *Oscinella frit*, 4 of *Oscinella vastator*, 5 of *Cctema* sp., 9 of *Opomyza germinationis* and 3 of Noctuidae (2 species). Reference back to Table III will show that these species are to be expected in a *Lolium* (or *Festuca*) ley.

Vertical Migration of Larvae of *O. frit*.

In the present studies, clumps of heavily infested tillers containing larvae of *O. frit* were placed, roots upward, at either 8-inch or 4-inch depths in earthenware pots which were filled with sandy, loam or clay soils. Star oats were then sown in the pots, which were sunk almost to the rim in bare soil. A large tub with a fine muslin top was put over each pot to prevent any possibility of direct oviposition on the tillers. The larvae were buried and oats sown on the 7th October 1953. Ten days later the oat cotyledons were showing, and, on the 30th October, deadhearts appeared and larvae were found in the tillers. When the oats were finally dug up and dissected on the 16th November, larvae were found in the oat tillers above the buried material that had been infested with larvae in all three soils and at both depths.

The factors influencing the migration of the larvae have yet to be studied in detail but will include the rate of decomposition of the buried host grasses and the thermal threshold of activity below which movement cannot take place. Chrzanowski (1931) has shown that activity in larvae of *O. frit* ceases at temperatures below 8°C. (46·4°F.) and this is in close agreement with D. Iley, working at the Field Station, who after laboratory experimentation used 7·2°C. (45·0°F.) as the thermal activity and developmental threshold of the larvae of the same species. The mean weekly soil temperature at a depth of 10 inches over a period of nearly four years is shown in fig. 1. At this depth, the mean temperature drops below the thermal threshold of activity between mid-October and mid-November and so the larvae are unlikely to leave their buried host-plants much

after that, although those on the way up would probably be able to continue during at least part of the day for a further period.

True larval diapause does not exist in these species, but the period of enforced hibernation when buried depends on the adjacent soil temperature and should continue, according to fig. 1, until about early April. Much of the buried grass will be at depths of less than 10 inches, where the soil will tend to warm

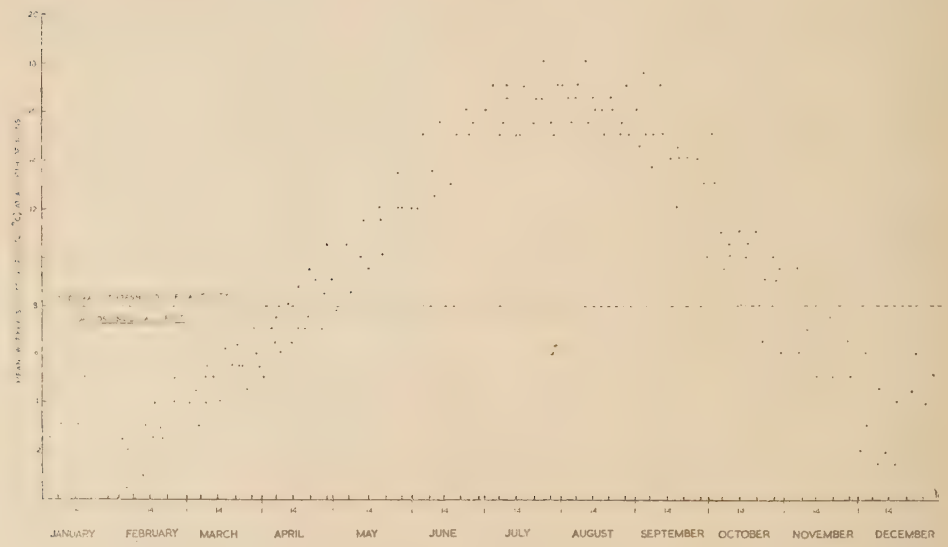


Fig. 1.—Scatter diagram of the mean weekly soil temperature (°C.) at a depth of 10 in. at Silwood Park, for the period 24th July 1950 to 29th April 1954.

up earlier in the year and have greater diurnal variation in temperature. Under these conditions, the larvae will appear in the tillers earlier. Fully developed larvae have been found in apparently healthy tillers of winter wheat in February, and this is probably due to their having entered the tillers in November and then remained dormant. Once the temperatures rise and the larvae commence feeding on the growing point, the deadhearts appear.

Stokes (1957) has shown that, in the laboratory, larvae of the wheat bulb fly exhibit a directional response towards a wheat-root diffusate. Whether this is also the case with larvae of other species, or whether the migration is purely random or coupled with a negative geotropism, remains to be determined.

Discussion.

The larvae found during the winter and spring within the basal tillers of autumn- and spring-sown cereals may be derived from one or more of three sources:

(i) Direct oviposition on or near the young cereal itself.

(ii) Oviposition on bare soil, usually before the cereal is sown.

(iii) Vertical migration of larvae, upwards from ploughed-in grasses.

In the first case, direct oviposition occurs in the autumn and may be due to a late generation of *O. frit*, which normally ceases oviposition by the end of September but in some mild seasons may continue on into October. More usually, *Opomyza florum* (F.), *Chlorops pumilionis* (Bjerk.) (the gout fly) and *Delia florilega* (Zett.) are responsible, since they normally oviposit during

October, and young cereals are then liable to direct attack. *Phorbia genitalis* (Schnabl & Dziedzicki) overwinters as a pupa, emerges early and oviposits during April, principally on wheat.

In the second case, *Leptohylemyia coarctata* (the wheat bulb fly) is usually responsible and oviposits during August on the bare soil of late summer fallows.

In the third case, not only leys but ploughed-in stubble containing grasses and volunteer cereals can act as a source of infestation. This accounts for the larvae of *Cetema*, *Meromyza*, *Opomyza*, *Geomyza* and *Oscinella* spp. found within the cereal when it has been sown after the flight period of the insect.

Laboratory experiments and field observations indicate that the larvae are not in general host specific and will feed to maturity within other grasses or cereals if these are reasonably succulent. It is thus the ovipositional preferences of the gravid females which cause the distribution of larvae of the different species among the grasses, as summarised in Table III. The host specificity in some cases is most marked. For example, what, one may ask, have *Holcus lanatus* and *Anthoxanthum odoratum* in common which is attractive to *Opomyza petrei* yet *Geomyza combinata* is attracted only to *H. lanatus* out of the pair? A whole series of such questions can be posed, and the study of some of these clear-cut cases should provide information as to what characters determine the attractiveness of a grass to a certain species of fly. A clue may thus be found to the requirements of *O. frit* which, owing to its lack of host specificity, would be a much more difficult species on which to start. Preliminary experiments on the tiller infestations of barley, oats, rye, wheat and maize clearly showed that *O. frit* will oviposit upon, and the larvae develop within, all five cereals in addition to the many wild grasses. This relatively wide host range probably accounts for there being no variety of oats at present available which shows any appreciable direct resistance to a tiller attack by *O. frit*. Until more is known about the factors attracting these flies, the chances of breeding directly resistant varieties appear to be slight.

Summary.

During the winter months, when larval populations of shoot flies (Diptera, Acalypterae) are relatively static, pure clumps of grasses in southern England were sampled. The tillers were dissected and the shoot-fly larvae removed and identified to determine what species were present and how and in what numbers they were distributed within the species of grasses. Concurrently, a permanent pasture was sampled in which the grasses were closely intermixed, and it was found in the two cases that the same host preferences of the insects were broadly maintained. Those preferences are due to the selectivity of the ovipositing female rather than the dietary requirements of the larvae, which are facultative parasites of most grasses and cereals.

A Table is given of the relative abundance of the larvae of 17 species in 16 different grasses and indicates the degree of host specificity of each insect. For example, *Oscinella frit* (L.), the frit fly of oats, is found in 11 of the common grasses but not in *Dactylis glomerata* whereas *O. albiseta* (Mg.) is found only in this grass.

Horizontal migration of larvae from tiller to tiller can take place; vertical migration may also take place from ploughed-in grasses to cereals sown above. It is shown that migration is mainly limited to autumn and spring when soil temperatures are above the thermal threshold of activity of the larvae.

Acknowledgements.

My thanks are due to Emeritus Professor J. W. Munro, Professor O. W. Richards and Dr. W. F. Jepson, of the Imperial College of Science and Technology and to Dr. William Davies, Director of the Grassland Research Institute,

for the opportunity of doing this work and for the facilities made available to me.

I am indebted to Miss V. V. Williams, who assisted throughout in the tedious dissection and counting of the numerous samples, and to Mr. A. J. Heard of the Grassland Research Institute for his co-operation in the sampling of the grass plots at Hurley.

This work was sponsored by the Agricultural Research Council, who provided the necessary grants.

References.

Chrzanowski, A. (1931). Ploniarka-mucha szwedzka (*Oscinis frit* L.), jej biologja, szkody zrzadzane przez nią w rolnictwie i jej zwalczanie. [*Oscinella frit* L., its biology, the damage caused by it in agriculture, and its control.]—*Chor. roś.* **1** pp. 23–55.

Cunliffe, N. (1921). Preliminary observations on the habits of *Oscinella frit*, Linn.—*Ann. appl. Biol.* **8** pp. 105–134.

Miles, H. W. (1921). Observations on the insects of grasses and their relation to cultivated crops.—*Ann. appl. Biol.* **8** pp. 170–181.

Nye, I. W. B. (1955). The external morphology and host relationships of some of the Dipterous larvae living in the Gramineae.—Ph.D. thesis, Univ. London.

Nye, I. W. B. (1958). The external morphology of some of the Dipterous larvae living in the Gramineae of Britain.—*Trans. R. ent. Soc. Lond.* **110** pp. 411–487.

Petherbridge, F. R. (1917). Frit fly (*Oscinis frit*) attacking winter wheat.—*Ann. appl. Biol.* **4** pp. 1–3.

Petherbridge, F. R. (1921). Frit fly (*Oscinis frit*) in winter wheat.—*Ann. appl. Biol.* **7** pp. 363–366.

Stokes, B. M. (1957). Laboratory experiments on larval behaviour of wheat bulb fly.—*Ann. appl. Biol.* **45** pp. 386–387.

© Commonwealth Agricultural Bureaux, 1959.

FURTHER OBSERVATIONS ON THE PERSISTENCE OF LARVICIDES AGAINST *CULICOIDES* AND A DISCUSSION ON THE INTERPRETATION OF POPULATION CHANGES IN THE UNTREATED PLOTS.

By D. S. Kettle, R. H. Parish and Jean Parish

Midge Control Unit, Department of Zoology, Edinburgh University.

Field trials to test the effectiveness of various larvicides against the larvae of the biting midge, *Culicoides impunctatus* Goetgh., in Scotland were conducted on Soutra Hill near Edinburgh during the winter of 1953/54. The results of these small-plot experiments have been reported in detail by Kettle, Nash & Hopkins (1956). They showed that the "immediate" control exerted by treatment was small but that after an interval of six months good "residual" control was obtained in most cases.

This delayed action of the larvicides was investigated and shown to be dependent upon local climatic conditions, particularly rainfall. It was considered that at least 20 in. of rain were necessary to distribute the insecticide throughout the top 2 in. of the soil and achieve good control of the larvae of *C. impunctatus* (Kettle & Parish, 1957).

During the autumn of 1955, some of these small field plots were re-examined to find out whether the larvicides were still effective two years after application. The results of this investigation, together with a discussion on the relationship between rainfall and larval control, have been detailed by Kettle & Parish (*ibid.*). Although the analysis of the data was complicated by a large natural reduction (76%) in the untreated plots, it appeared that after allowing for decreases in the untreated plots and using grouped data, the following larvicides were still active two years after application:—DDT applied as a dust, wettable powder or water-miscible concentrate at 50 and 200 mg. p,p′DDT/sq. ft.—99 per cent. control; BHC as a wettable powder at 50 and 200 mg. γ BHC/sq. ft. and water-miscible concentrate at 200 mg. γ BHC/sq. ft.—95 per cent. control; dieldrin at 25 mg./sq. ft.—97 per cent. control; and chlordane at 50 mg./sq. ft.—84 per cent. control.

All these treatments and some others were re-sampled in the first three months of 1957 to determine the degree of control being exerted three years after application.

During the autumn of 1955, additional field trials were carried out on Soutra Hill to determine the effect of spray volume upon insecticidal effectiveness (Kettle & Parish, *ibid.*). The results of these trials indicated that, with DDT, moderate spray volumes (15 and 25 gal./acre) gave the best control at the same insecticide dosage. However, it was concluded that the volume of spray was unimportant provided uniform coverage was obtained.

During 1957 (January–March) the 12 small plots used in this experiment were also re-sampled to find out if the spray volume had any effect upon insecticide persistence.

This paper presents the results of these additional observations on both trials.

The techniques used were the same as those described in the earlier papers (Kettle, Nash & Hopkins, 1956; Kettle & Parish, 1957) except that the individual soil samples were placed in separate polythene bags.

Before presenting the results so obtained it will be useful to consider the changes that occurred in the larval populations of the untreated plots and to decide what allowances must be made for them when assessing the control achieved by each treatment.

Population Fluctuations and Calculation of Control achieved.

Insect populations are often subject to very wide fluctuations. It is usual, therefore, in most experiments on control to include a number of untreated checks, which will provide estimates of natural fluctuations in the insect population. To meet this requirement, nine untreated plots were incorporated in the experimental design on Soutra. Of these, five were on site 1 and four on site 2.

Soutra 1, 1953/54.

Pre-treatment sampling of Soutra 1 was carried out in autumn 1953. The 45 samples collected from the five untreated plots yielded 102 larvae (= 2·27 larvae/sample). In winter (January–March) 1954 the same five plots provided 247 larvae from 60 samples, giving an average of 4·12 larvae/sample and an increase of +81 per cent. This increase is statistically highly significant ($P < 0{\cdot}001$) but its biological interpretation is not very obvious. This difficulty was referred to in an earlier paper (Kettle, Nash & Hopkins, 1956, pp. 562–5) when its consideration was left until later. The time has now come when an answer to this problem must be attempted.

It might be suggested that there had been a change in technique, so that a larger proportion of the larval population was being recovered. In fact, there was a change in the technician concerned with soil washing but it was a change from an experienced to an inexperienced worker, which was more likely to result in the recovery of a lower proportion of larvae than a higher.

As there was no change in technique, we must consider whether this observed change in the larval population density represented a real or an apparent increase. But before doing so it will be useful to review the known facts of the life-history of *C. impunctatus*.

C. impunctatus is considered to have one generation a year (Hill, 1947). Individual adults live for about two weeks, while the seasonal period of adult activity lasts from May to September, inclusive. The females lay batches of eggs from which larvae emerge. These pass through four instars before finally pupating on the soil surface during the following summer. From October until April the larval population would be expected to remain fairly constant. It would be reduced by natural larval mortality and increased by the addition of larvae newly emerged from eggs.

Hill (1947) gives the duration of the egg stage in *C. impunctatus* as 7–20 days at 16–20°C. (= 61–68°F.) and Parker (1950) as 7–9 days at 19–21°C. (= 66–70°F.). Parker (*ibid.*) points out that this time is the slowest of the seven species of *Culicoides* on which he made observations (excluding *C. grisescens* Edw. which hibernates in the egg stage). Mean daily temperatures in excess of 60°F. are unlikely to be very frequent, especially towards the end of the summer, at Soutra which is 1,100 ft. above mean sea level. Hence it is not beyond the realms of possibility that some eggs might hatch late in the autumn and increase the larval population. If such a hatching had occurred between the pre- and post-treatment samplings of 1953/54, more early-stage larvae would be expected to occur in the later samples. In the event, only three second-stage larvae were found in each group. The percentage of early instar (2nd & 3rd) increased from 30 per cent. to 39 per cent. but the difference was statistically insignificant ($P = 0{\cdot}1$–$0{\cdot}2$). There is no evidence, therefore, to attribute the increase in larval population to delayed hatching of eggs, and therefore no evidence that this is a real population increase.

In between these two groups of observations one important event had occurred, namely the application of various insecticides to most of the plots under observation. It is possible that larvae might have been irritated by the chemicals and moved away from the treated plots. Here it should be remembered that each plot was 10 yd. × 10 yd. while an average larva is only 5 mm. (= 1/5th in.) long, so that a larva might have to make a comparatively very long journey before reaching untreated soil even if it knew in which direction to move. Nevertheless, the repellent effect of sublethal doses of DDT is a well-known phenomenon in insects (Kennedy, 1947).

Support for this view is given by Table I, where the plots have been arranged in four groups depending upon whether they have received no treatment, treatment with oil solutions—which because of their inability to mix with water are

TABLE I.

Numbers of larvae of *C. impunctatus* recovered from experimental plots on Soutra Hill, site 1. Plots grouped according to treatment.

Treatment	No. of plots	Nov.–Dec. 1953	Jan.–May 1954	Difference (%) + —	Nov./54–Jan./55	Difference (%) + —
None	5	102	185 (247)	81	218	114
Oil solution	8	217	309 (412)	42	274	26
Other preparations (3 & 6 mg./sq. ft.)	7	230	303 (404)	32	436	90
Other preparations (12 mg./sq. ft. and over)	17	400	348 (464)	13	196	51
Total	37	949	1145 (1527)	21	1124	18
No. of samples ..	—	333	444		333	
Larvae/sample ..		2·85	3·44	(*P* <0·001)	3·37	(*P* almost 0·001)

Each value represents the number of larvae found in nine samples from each plot. In Jan.–May 1954, 12 samples were taken and the actual total is given in brackets. Percentage differences refer to Nov.–Dec. 1953.

likely to be ineffective, and low or high dosages of other preparations. Certainly there is a negative correlation between the potential insecticidal capacity of a group and the population increase. This could be due either to movement away from the treated plots or to mortality caused by treatment. To attribute this to mortality leaves the apparent population increase unexplained. But is the repellency explanation correct?

There is one strong piece of evidence against this view. The experimental site did not utilise all the breeding area of *C. impunctatus* so that larvae, repelled by the treatment applied to the plot in which they happened to be, could either enter other experimental plots or leave the experimental site altogether. Since this repellency movement would be in addition to normal larval movements, one would expect rather more larvae to leave the site than to enter it. In other words, the total larval population would be expected to decrease. In point of

TABLE II.

Numbers of larvae of *C. impunctatus* recovered from three samples taken from each plot on Soutra Hill, site 1, which was sampled in two sections, A & B.

Section A		Pre-treatment			Post-treatment				
Treatment DDT and γ BHC (mg./sq. ft.)	No. of plots	1 3.xi.53	2 16.xi.53	3 27.xi.53	4 11.i.54	5 18.ii.54	6 29.iii.54	7 29.iv.54	
i. None	3	30	12	14	57	28	44	27	
ii. Dust (3 highest)	6	60	34	38	59	52	79	39	
iii. Oil 50,200	4	13	16	30	45	9	54	39	
iv. w.p. 50 + w.m.c. 12	4	33	17	32	20	39	15	33	
Total	17	136	79	114	181	128	192	138	
Larvae/sample		2·67	1·55	2·24	3·55	2·51	3·76	2·71	$t0{\cdot}05S_{\bar{x}}$ ±0·80

Section B		Pre-treatment			Post-treatment				
		10.xi.53	23.xi.53	3.xii.53	18.i.54	24.ii.54	2.iv.54	5.v.54	
i. None 2 plots + Dust 3 mg. 2 plots	4	32	19	30	66	35	84	38	
ii. Oil 3, 12	4	65	28	65	71	54	51	89	
iii. w.p. 3, 12, 200	6	49	30	49	61	9	35	39	
iv. w.m.c. 3, 50, 200	6	100	64	89	70	37	66	83	
Total	20	246	141	233	268	135	236	249	
Larvae/sample		4·10	2·35	3·88	4·47	2·25	3·93	4·15	$t0{\cdot}05S_{\bar{x}}$ ±0·74

w.p. = wettable powder; w.m.c. = water-miscible concentrate. $t0{\cdot}05\ S_{\bar{x}}$ = difference between means at 5 per cent. level of significance. Treatment applied 15th–18th December 1953.

fact it increases by 21 per cent. from 2·85 larvae per sample to 3·44 and statistically this is highly significant ($P < 0{\cdot}001$). It must be concluded that repellency does not explain the observed population increase.

There are some other data that are relevant to this discussion. There were 37 plots to be sampled on site 1, and, in order that samples should be examined as soon as possible after collection, the site was divided arbitrarily into two sections, A and B, which were sampled alternately, section B being sampled about a week later than section A. When the site was first marked out, the plots were numbered consecutively from 1 to 37 and for this sub-division plots 1 to 17 were allocated to section A and plots 18 to 37 to section B. The untreated controls were shared between the sections, 3 in A and 2 in B. As similar treatments with DDT and γ BHC had been put side by side, they occurred in the same section. Each section was sampled three times before treatment. The data were subjected to a fuller analysis of variance than that already published and showed that there were highly significant differences ($P < 0{\cdot}001$) between the pre-treatment samplings (Table II). This means that there were significant fluctuations in larval density between the sampling occasions.

It is important to find out if this is a general character of the plots or if it is due to large changes in a few plots. Unfortunately there is such a big variation between individual samples from the same plot that the three samples collected on each occasion were inadequate to reveal general trends in individual plots (see Tables IV & V, pp. 560–1, in Kettle, Nash & Hopkins, 1956). Some method of grouping the plots is required, and in this case the obvious way is to group the plots according to their *subsequent* treatment. (The treatments had been assigned at random.) This gave groups containing 2 to 6 plots. It was considered that a group of only two plots (6 samples per occasion) was still too small for this analysis and therefore the two small groups of section A (wettable powder 50 mg./sq. ft. and water-miscible concentrate 12 mg./sq. ft.) were

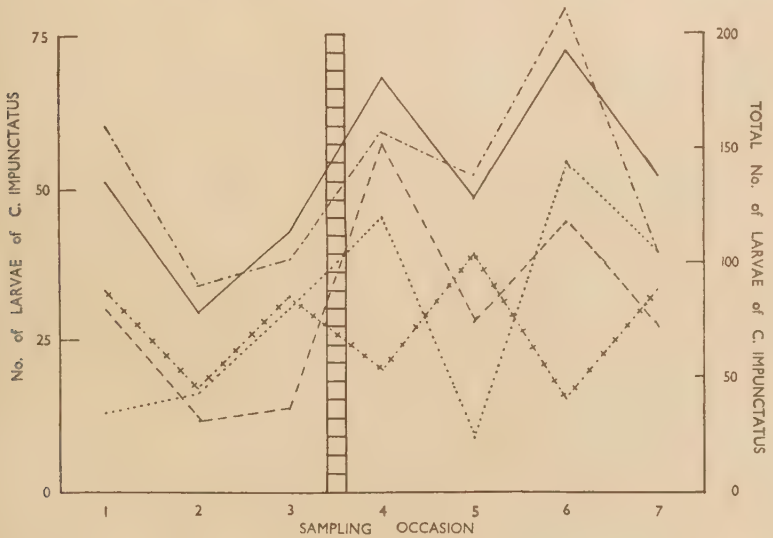


Fig. 1.—Numbers of larvae of *C. impunctatus* on different sampling occasions, Soutra 1, section A. Totals given by continuous line and right-hand scale. Group scale on left: i, broken line; ii, dash dot line; iii, dotted line; iv plus dot line. Data from Table II. Boxed column represents application of insecticide.

amalgamated to give a group of four plots. For the same season the two untreated plots and the two dust treatments (3 mg./sq. ft.) were combined in section B.

The grouped data are presented in figs. 1 & 2 and Table II. They show that large changes in larval density occur frequently in all groups. But of greater importance is the demonstration that in nearly all groups the changes between successive sampling occasions are similar in both magnitude and direction. This strongly suggests that the larvae are responding to some factor or group of factors which operate widely throughout the site.

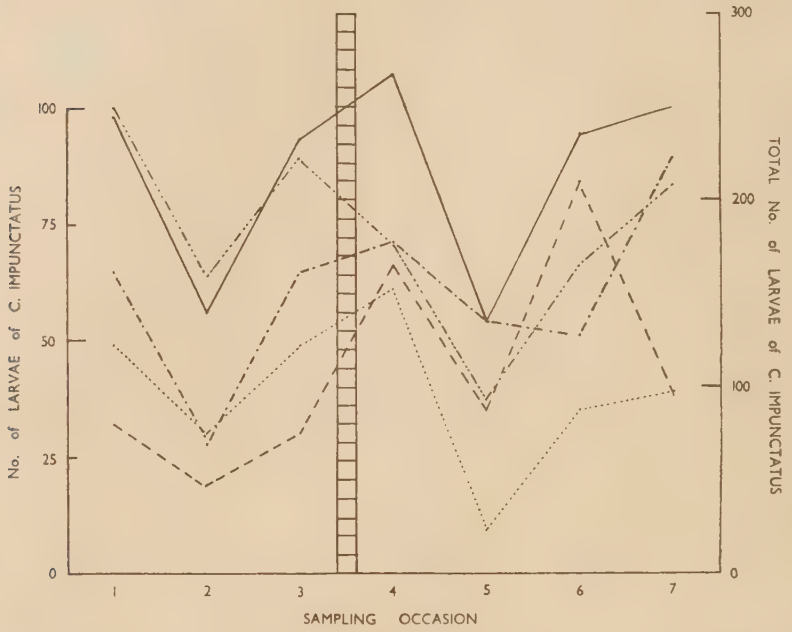


Fig. 2.—Numbers of larvae of *C. impunctatus* on different sampling occasions, Soutra 1, section B. Data from Table II. Dash, three dots line represents group iv. For other symbols, see fig. 1.

There are seven observations in each section and it is remarkable that of the six changes in larval population between consecutive samplings five of them in section A and four in B (*i.e.*, 9/12 in all) should exceed the 5 per cent. level of significance. Given the existence of such wide-scale natural fluctuations in apparent larval density it is easy to understand how it is possible to obtain a significant difference in population density between any two groups of samplings (*e.g.*, pre- and post-treatment). Moreover, the fact that all the plots seem to fluctuate in unison emphasises the importance of having untreated plots which will act as indicators of these fluctuations and provide estimates of their magnitude.

The question now arises as to where the larvae go when the population apparently declines or, looked at in another way, where the larvae come from when the population increases. Before an answer is suggested it is necessary to outline the mode of sampling adopted. The vegetation within a plot is likely to vary from flat swards of *Sphagnum* or *Polytrichum* to dense tussocks of *Eriophorum vaginatum* or *Calluna vulgaris*. Previous experience had led one to

associate certain vegetational cover with larvae of *C. impunctatus* and the sampling was randomised not throughout the plot as a whole but throughout the area regarded as suitable. As a check on the consistency of this outlook, a note was made of the vegetational zone from which each sample was taken. Examination of these notes (Table III) shows that there was reasonable consistency in the vegetation sampled. Hence these fluctuations cannot be attributed to biased sampling.

TABLE III.

Dominant vegetation of samples taken from Soutra Hill, site 1.

Sampling occasion	1 *Sphagnum*	2 *Polytrichum*	3 *Polytrichum* and *Sphagnum*	4 No moss	5 Total with *Sphagnum*	6 Total with *Polytrichum*
Before treatment						
1 (3 & 10.xi.53)	53	8	41	9	94	49
2 (16 & 23.xi.53)	80	3	26	2	106	29
3 (27.xi. & 3.xii.53)	78	2	28	3	106	30
After treatment						
4 (11 & 18.i.54)	73	4	33	1	106	37
5 (18 & 24.ii.54)	63	10	36	2	99	46
6 (29.iii. & 2.iv.54)	63	13	29	0	92	42
7 (29.iv. & 5.v.54)	82	5	24	0	106	29

There were 111 samples taken on each occasion, but on the sixth, records were kept for only 105. Columns 4–6 are the more important since changes in 1 and 2 are often balanced by opposite changes in 3.

This restricted random sampling offers an answer to our problem. If under certain conditions, as yet unknown, larvae can move from "suitable" to "unsuitable" areas, then the larval density in the "suitable" area will fluctuate with these unknown conditions. One factor which might produce this effect would be the soil water level. Under "normal" conditions larvae might congregate in zones of moderate water content. Then as the water level rises they would tend to move into the zone which was previously too dry. Similarly, as the water table drops, the larvae would be likely to move into zones which are ordinarily too wet. The frequency of the larval fluctuation is evidence that the factor concerned is commonly encountered.

In this connection it is interesting to note that these fluctuations are more marked in parts of the site where the ground is particularly uneven, consisting of tussocks of *Calluna vulgaris* and *E. vaginatum*. Under these conditions, providing the larvae maintain their position relative to the soil surface, a comparatively small lateral movement would carry them into a drier or wetter habitat. Alternatively, they could follow the soil water by vertical movements up and down in the soil. This would be physically more difficult than lateral movement because in most samples there is a marked change in texture at a depth of about two inches, below which the peat is more densely packed.

A consideration of the methods of storage and examination of the samples, after collection, has some bearing on this point. After collection, the samples were placed in a closed half biscuit tin and kept under cool conditions in an unheated room until required for examination. On the average a sample would be kept for two days. It was under similar conditions to these that Kettle &

Lawson (1952, Table II) found over 96 per cent. of the larvae of *C. impunctatus* in the top two inches. This observation can be interpreted in two ways. Either the larvae rarely go deeper than two inches or they move upwards under the conditions of storage. This movement would presumably be in response to some change in conditions, such as the high humidity in the storage tin, where the air is virtually saturated. In the work being considered here, only the top two inches were examined, but the majority of the samples extended much deeper (4–6 inches). So that if, in the field, the larvae had reacted to the unknown factor by moving deeper into the soil they would still be likely to be in the sample when collected. Under the constant conditions of storage they would probably make their way up to the top two inches. The fact that on occasions a whole batch of samples could show low larval densities after this procedure suggests that the "missing" larvae were not in any part of the sample. Either they had moved laterally out of the area regarded as "suitable" for sampling or they had gone deeper than the sample. Of these two alternatives, lateral movement seems the more acceptable.

There is something ironic about the fact that in spite of insecticidal treatments, some of which have been shown (Kettle, Nash & Hopkins, 1956) to have given highly significant reductions in larval densities over the period, the populations in both sections of site 1, as a result of larval movement, were virtually the same on the last occasion (late April–early May) as on the first (early November). Section A produced 136 larvae in November and 138 in April, while the comparable figures for section B are 246 and 249 (Table II).

Soutra 2, 1954.

The other site on Soutra Hill was sampled over a shorter period than site 1, from the middle of March to the end of May 1954. Nevertheless it will be interesting to compare these data with those already considered.

The larval density in the untreated plots was 4·64 larvae/sample before the spraying date and 5·28 afterwards, an increase of +14 per cent. which is statistically insignificant ($P = 0{\cdot}4$). The 26 plots comprising the whole of site 2 yielded 1,299 larvae (= 5·55/sample) before and 943 larvae (= 4·03/sample) after treatment—a reduction of 27·4 per cent. (data from Kettle, Nash & Hopkins, 1956, Table X, p. 567). The experimental plots on this site were arranged in small groups (2, 3 or 4) separated by relatively deep, wide drainage channels which were likely to prevent larvae moving from one group to another. Hence any repellency effect would tend to drive larvae out of the sampled area rather than from one

TABLE IV.

Relative abundance and stage of growth (instar) of larvae of *C. impunctatus* on different sampling occasions in 1954 on Soutra Hill, site 2.

Date	No. of samples	Calculated no. of larvae in 75 samples			
		2nd	3rd	4th	Total
10 March ..	72	2	126	261	389
17 „ ..	84	4	159	207	370
23 „ ..	87	14	180	243	437
2 April ..	9	25	133	300	458
			Treatment applied		
12 May ..	78	17	65	202	284
19 „ ..	78	10	37	233	280
26 „ ..	78	13	31	300	344

plot to another within it. This does not mean that the observed reduction was due to repellency although the latter could have been a contributory factor. As stated earlier (p. 65) the small size of the larva, compared with the relatively large area sprayed, is likely to preclude the possibility of successful escape from the treated plot for all except a few larvae on the periphery.

The numbers of larvae and their instar distribution for each sampling occasion are recorded in Table IV and fig. 3. After spraying, there was a reduction in the total number of larvae. With the normal seasonal increase in temperature aiding growth in May there was a steady decrease in the number of third-stage larvae, coinciding with an increase in those in the fourth instar. One surprising feature

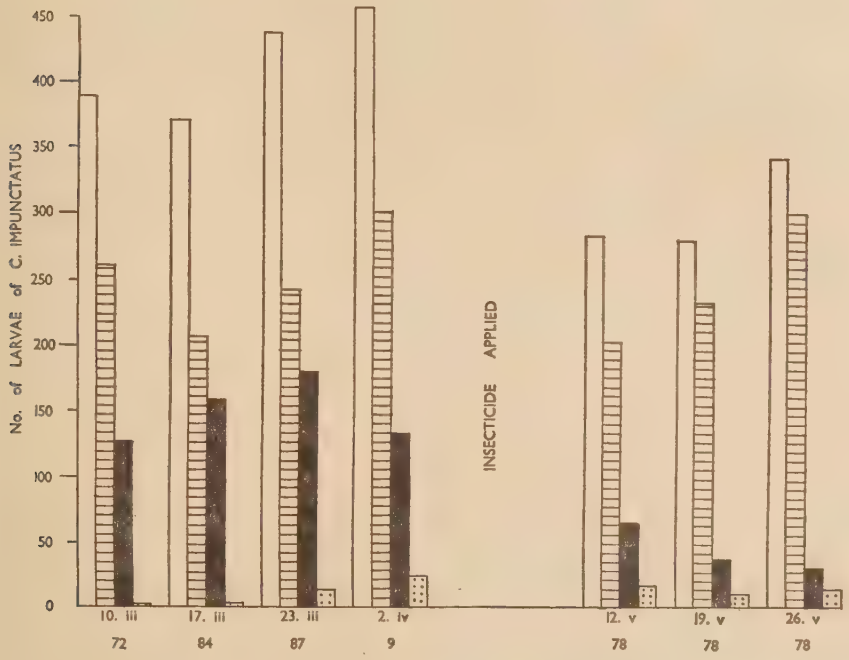


Fig. 3.—Numbers of larvae of *C. impunctatus* in 75 samples on different sampling occasions, Soutra 2. Figures below dates refer to numbers of samples actually examined. Totals, open column; 4th instar, hatched column; 3rd instar, solid column; 2nd instar, dotted column.

is the increase in the number of second-stage larvae before the onset of any adult emergence (*cf.* 10th and 17th March with 23rd March and 2nd April in Table IV). This is suggestive of delayed hatching in a small proportion of eggs but more data are needed.

An analysis of variance was made of all the available pre-treatment data, which were classified according to the date of sampling. No attention was paid to the source of the samples within the site. This analysis failed to detect any significant difference between the pre-treatment sampling occasions. However, such a difference could have been masked by differences within the site. The pre-treatment sampling of the plots on this site was not as regular as on site 1 and only 14 plots were sampled on every occasion, except 2nd April. In Table V

they have been grouped according to their subsequent insecticidal treatment in three sets—aldrin and dieldrin, malathion (2 preparations) and the rest (DDT, BHC and chlordane). The results are plotted in fig. 4 and once again the larval

TABLE V.

Numbers of larvae recovered from three samples taken from each plot on Soutra Hill, site 2 in Mar.–May 1954.

Treatment (mg./sq. ft.)	No. of plots	Pre-treatment			Post-treatment			Total larvae
		1 10.iii.54	2 17.iii.54	3 23.iii.54	4 12.v.54	5 19.v.54	6 26.v.54	
i. Aldrin 6, 12 Dieldrin 6, 12	4	63	48	113	31	54	61	370
ii. Malathion w.p. 3, 12 ,, e.l. 3,12,50	5	62	70	76	22	31	44	305
iii. DDT 50 BHC 12, 50 Chlordane 6, 25	5	83	92	103	68	89	57	492
Total	14	208	210	292	121	174	162	1167
Larvae/sample		4·95	5·00	6·95	2·88	4·14	3·86	$t0{\cdot}05S_{\bar{x}}$ $\pm 1{\cdot}29$

e.l. = emulsifiable liquid; other symbols as in Table II.

density appears to fluctuate from occasion to occasion with similar changes being shown by all groups. Analysis now reveals significant differences between the pre-treatment sampling occasions (Table V). The third (23.iii.54) differs significantly from the first and second, but this is entirely due to a sharp rise in group i (aldrin and dieldrin) while the other groups increase but slightly.

This finding has a bearing on the explanation advanced above for apparent fluctuations in larval density. Most of the plots on site 2 are placed on ground where the bogland is passing over to acid grassland, and carry a cover of *Juncus effusus*, *Deschampsia caespitosa*, *Festuca tenuifolia* and *Agrostis canina*. One small part of the site retains the more familiar cover of large clumps of *E. vaginatum* which dominated site 1. It is here that the aldrin and dieldrin treatments of group i were applied and here that population fluctuations were most marked. This provides support for the idea of an association between tussock-strewn ground and fluctuations in larval density.

Soutra 1, November 1954–January 1955.

In these samplings there was a highly significant ($P < 0{\cdot}001$) increase in the untreated plots of +114 per cent. compared with the pre-treatment density (Table I). However, we are now dealing with a new generation of *C. impunctatus*, and there is no reason why the larval population should not be larger than its predecessor. Clearly, the differences between two generations will depend upon numerous factors, especially those affecting the length of life and mortality of the adults and the availability of blood for the females.

Soutra 1 and 2, October 1955.

Following the hot, dry summer of 1955, the larval population in the untreated plots in October 1955 had fallen to about a quarter of its previous value in November 1954–January 1955 (from 143 to 30 on site 1 and 144 to 39 on site 2) (Tables VI & VII, bottom three sections). This new density was approximately half the original value in November–December 1953 when the same plots yielded,

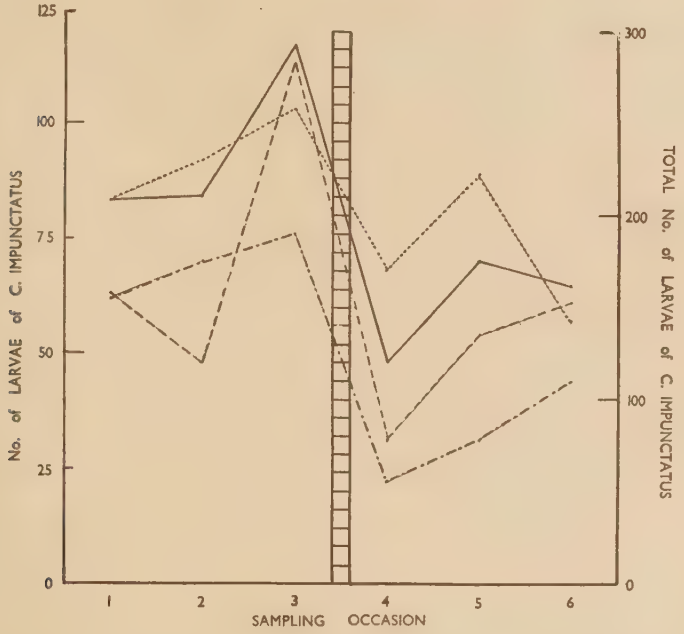


Fig. 4.—Numbers of larvae of *C. impunctatus* on different occasions, Soutra 2. Data from Table V. For other details, see fig. 1.

on site 1, 66 larvae as compared with 30, and in March 1954 on site 2, 75 as compared with 39. The Soutra sites are readily affected by prolonged drought as they are placed on a saddle (1,100 ft. a.m.s.l.) which receives drainage from two slightly higher hills to the south (Dun Law, 1,292 ft.) and north (Soutra, 1,209 ft.), while it drains away into two deep valleys to the east (Linn Dean Water) and the west (Armet Water).

Soutra 1 and 2, January–March 1957.

The summer of 1956 was wet, and the larval population in January–March 1957 had recovered a little. Compared with the previous overwintering population, sampled in October 1955, it had increased from 30 to 36 in the three plots of site 1 (Table VI) and from 39 to 48 in the two plots of site 2 (Table VII), giving an overall increase from 69 to 84 (= +22 per cent.). Even so the population was still only about half its original density in November–December 1953. Then the five untreated plots of site 1 had produced 102 larvae compared with 54 in January–March 1957 and on site 2 the corresponding figures for four untreated plots were 167 larvae in 1953 and 69 in 1957. For the nine plots this gives comparative larval densities of 269 and 123 for 1953 and 1957, respectively.

TABLE VI.

Persistence of insecticides on Soutra Hill, site 1. Numbers of larvae found in 9 samples.

Insecticide	Preparation	Dosage (mg./sq. ft.)	Nov.–Dec. 1953	Per cent. control		Jan.–Mar. 1957		
				Nov. 1954–Jan. 1955	Oct. 1955	No. larvae	No. expected	Per cent. control
p,p′DDT	Wettable powder	12	15	(80) 91 } 97	*	2	7·9	75 } 94
		50	27	(96) 98 }	100	0	14·3	100 }
		200	28	(100) 100 }	100	0	14·8	100 }
p,p′DDT	Water-miscible concentrate	12	15	(93) 97 } 98	*	0	7·9	100 } 100 } 98
		50	42	(95) 98 }	100	0	22·2	100 }
		200	28	(100) 100 }	92	0	14·8	100 }
p,p′DDT	Dust	12	15	(93) 97 } 98	*	0	7·9	100 } 100 }
		50	20	(90) 95 }	100	0	10·6	100 }
		200	42	(98) 99 }	100	0	22·2	100 }
γ BHC	Wettable powder	12	19	(26) 66 } 87	*	11	10·1	Nil } 41
		50	22	(86) 94 }	*	0	11·6	100 }
		200	20	(100) 100 }	79	8	10·6	24 }
γ BHC	Water-miscible concentrate	50	38	(Nil) 43 } 61	*	10	20·1	50 } 59 } 50
		200	18	(94) 97 }	100	2	9·5	79 }
Untreated. Nos. of larvae only			20 } 66	34 } 143	0 } 30	13 } 36	Control corrected for changes in untreated plots except for figures in brackets.	
			30 }	55 }	4 }	9 }		
			16 }	54 }	26 }	14 }		
			21	5	*	4		
			15	70	*	14		
Total untreated			102	218	*30*	54	* Not sampled. Figure in italics indicates incomplete total.	
Percentage of Nov.–Dec. 1953			100	214	45	53		

This recovery is less than one might have anticipated. Several factors could have contributed to this finding. Firstly, the population of *C. impunctatus* on Soutra is restricted to a comparatively small isolated patch of bogland in the midst of acid grassland. Hence recolonisation from other breeding grounds, less adversely affected by the 1955 drought, would be negligible. Secondly, the population has suffered from the application of insecticide to some of its better breeding grounds. As a rough estimate, perhaps as much as 5 per cent. of the potential breeding grounds received treatment. Thirdly, the recovery of a population can be achieved either by increasing its density per unit area or by extending its area of breeding. In the present instance the sampled (experimental) area was not sufficiently representative of the whole area to give an accurate picture of changes in breeding area. For example, it does not include any samples from the surface of the nearby raised bog, which had been found on a previous occasion to carry a low density of larvae of *C. impunctatus*.

Conclusions.

The conclusion to be reached from this analysis is that although large fluctuations in the larval population occur, they are to be attributed to unknown natural environmental variables and not to any repellent effect of treatment. That is to say, there is no reason to suspect the independence of the untreated plots, and they remain the most satisfactory method of assessing natural changes in density.

If it is decided to take no account of increases in the untreated larval density, then one under-estimates the degree of control obtained, but no real harm is done. On the other hand, to ignore decreases in the checks is to over-estimate the efficiency of a treatment, and this might lead to erroneous conclusions. In the following section, allowance has been made for the decreasing larval density.

Larval Observations, January–March 1957.

Persistence of DDT and BHC.

The results of re-sampling Soutra 1 are given in Table VI. Of the nine DDT treatments, eight are still exerting complete larval control while one (wettable powder 12 mg. p,p′DDT/sq. ft.) produced 75 per cent. larval reduction. It is very satisfactory that these treatments should be so effective three years after application. The dust and water-miscible concentrate preparations appear to be slightly more effective than the wettable powder but this is decided solely by the single relative failure. At reasonable dosages (50 mg./sq. ft.) the preparations are equally potent.

The γ BHC results are less satisfactory. Only one treatment (wettable powder 50 mg. γ BHC/sq. ft.) was completely effective and one had ceased to exert any control. There is no doubt of the superiority of DDT over BHC as a larvicide for *C. impunctatus*. In addition, with passage of time, the BHC treatments appear to be losing their potency. Thus, one year after application, the five BHC treatments achieved 74 per cent. control * but two years later only 50 per cent. This reduction is wholly due to the wettable powder, which declines from 87 * to 41 per cent., while the water-miscible concentrate stays steady at 61 * and 59 per cent.

The results on Soutra 2 (Table VII) support these comments. Thus the heavier DDT treatment (50 mg. p,p′DDT/sq. ft.) continues to exert complete control but once again the lower dosage of wettable powder (12 mg. p,p′DDT/sq. ft.) has become less effective with the passage of time, declining from 56 per cent. to 22 per cent. The latter's failure accounts for the drop shown by the combined DDT results (80 to 66 per cent.) for the absence of any noteworthy

* Larval increase in untreated plots allowed for.

TABLE VII.

Persistence of insecticides on Soutra Hill, site 2. Numbers of larvae found.

Insecticide	Dosage (mg./sq. ft.)	March 1954	Per cent. control		Jan.–Mar. 1957		
			Nov. 1954–Jan. 1955	Oct. 1955	No. larvae	No. expected	Per cent. control
Dieldrin wettable powder	3	41	(61) 76	*	8	16·9	53
	6	49	(80) 87	*	2	20·2	90
	12	44	(45) 66 } 83	*	0	18·2	100 } 88
	25	72	(89) 93	97	0	29·7	100
Chlordane water-miscible concentrate	6	78	(46) 67	*	23	32·2	29
	12	48	(46) 67	*	4	19·8	80
	25	60	(42) 64 } 68	*	5	24·8	80 } 65
	50	38	(66) 79	85	0	15·7	100
p,p′DDT wettable powder	12	28	(29) 56 } 80	*	9	11·6	22 } 66
	50	36	(97) 98	100	0	14·9	100
γ BHC wettable powder	12	58	(71) 82 } 89	*	11	24·0	54 } 63
	50	46	(96) 97	100	5	19·0	74
Untreated. Nos. of larvae only		63	71	*	14	For details see Table VI.	
		29	56	*	7		
		16 } 75	46 } 144	2 } 39	3 } 48		
		59	98	37	45		
Total untreated		167	271	*39*	69		
Percentage of March 1954		100	162	52	41		

difference between p,p′DDT and γ BHC (66 as compared with 63 per cent.). Both the γ-BHC treatments have deteriorated over the two years, falling from 82 to 54 per cent. and from 97 to 74 per cent., respectively, for applications of 12 and 50 mg. γ BHC/sq. ft.

When the observations on p,p′DDT for both sites were combined, it was found that only 11 larvae were recovered from the 11 treated plots in place of the expected 149, a reduction of 93 per cent., whereas after the same combination the seven γ BHC-treated plots yielded 47 larvae in place of an expected 105, a reduction of 55 per cent.

Persistence of dieldrin and chlordane.

During the two years since the dieldrin-treated plots were last sampled, the insecticide has increased in effectiveness (Table VII). The three highest dosages (6, 12 and 25 mg./sq. ft.) all gave very good control, while the lowest dosage (3 mg./sq. ft.) has declined a little. If the larval increase in November 1954–January 1955 is taken into account, then the lowest dosage has declined from 76 to 53 per cent. control; the 6 mg./sq. ft. treatment remains almost steady at 87 to 90 per cent., while the two higher dosages have improved from 66 and 93 to 100 per cent. Clearly, dieldrin is a very useful larvicide for *Culicoides*.

The picture for chlordane is very similar, with improving control in the three highest dosages but not in the lowest, which declines. Again, if the larval increase is allowed for, the lowest dosage has dropped from 67 to 29 per cent. but the other three have still improved, 67 to 80, 64 to 80 and 79 to 100 per cent. Chlordane is not so effective as dieldrin, which produces complete control at 12 mg./sq. ft., but is comparable to DDT as it gives complete control at 50 mg./sq. ft.

The improvement in degree of control attained by dieldrin and chlordane between the first and third years after application is particularly interesting.

TABLE VIII.

Influence of spray volume on persistence and effect of DDT, Soutra Hill, site 1.

Spray volume (gals./acre)	No. larvae Nov. 1954–Jan. 1955	Per cent. control Oct. 1955	Jan.–Mar. 1957		
			No. larvae found	No. larvae expected	Per cent. control
5	71	18	0	18	100
10	50	8	16	13	Nil
15	66	81 } 43	1 } 18	17 } 105	94 } 83
25	93	86	0	23	100
50	33	25	1	8	88
80	105	20	0	26	100
Untreated	34	0	13		
Nos. of larvae only ..	55	4	9		
	54	26	14		
Total untreated ..	143	30	36	Treated plots received 50 mg. p,p′DDT/sq. ft. on 29th April 1955.	
Percentage of Nov. 1954–Jan. 1955	100	21	25		

The insecticides were applied in April 1954. Between then and the end of October 1954, 24·28 inches of rain were recorded at the Royal Observatory, Edinburgh. (According to the rainfall map of Great Britain published by Director General, Ordnance Survey, 1949, the Royal Observatory has an average annual rainfall of 27·5 inches and Soutra Hill of 35 inches—about 25 per cent. more.) This rainfall was adequate for p,p′DDT and γ BHC to attain full affect but not for dieldrin and chlordane. Presumably this reflects the comparative rates at which these insecticides are carried down into the larval habitat by rainfall.

TABLE IX.

Influence of spray volume on persistence and effect of DDT, Soutra Hill, site 2.

Spray volume (gals./acre)	No. larvae Nov. 1954–Jan. 1955	Per cent. control Oct. 1955	Jan.–Mar. 1957		
			No. larvae found	No. larvae expected	Per cent. control
5	46	27	0	15	100
10	54	8	0	18	100
15	52	−83 (−1)	0 (1)	17 (104)	100 (99)
25	92	64	1	31	97
50	36	11	0	12	100
80	32	−125	0	11	100
Untreated Nos. of larvae only	46 98	2 37	3 45		
Total untreated ..	144	39	48	Treated plots received 25 mg. p,p′DDT/sq. ft. on 30th June 1955.	
Percentage of Nov. 1954–Jan. 1955	100	27	33		

Spray volume and insecticidal effectiveness.

The additional observations on the spray-volume experiments are recorded in Tables VIII and IX. Both series of tests (25 and 50 mg. p,p′DDT/sq. ft.) show increased larvicidal activity. This is most marked in the lower dosage which in a year has changed from completely ineffective to producing 99 per cent. control. The heavier application has appreciated from 43 to 83 per cent. control, but its failure to do better is entirely due to one plot (10 gal./acre) which gave no control at all. If that is excluded, the higher dosage gave 98 per cent. control. Apart from this example, all the other treatments were highly successful, only the occasional larva being found. This confirms the conclusion reached earlier (Kettle & Parish, 1957) that spray volume in itself is unimportant, providing that the coverage is adequate.

In these experiments, as in those of the previous section, there has been considerable improvement in control with the passage of time, and again it can be associated with the need for large amounts of rain to wash the insecticides down to the larvae. Between the application of the lower dosage of DDT and the first post-treatment sampling only 3·82 * inches of rain fell and no control

* All rainfall figures refer to the Royal Observatory, Edinburgh, unless otherwise stated. This information was made available by courtesy of the Officer-in-charge, Meteorological Office, Edinburgh.

was achieved, but after a further 34·38 inches had fallen in the next 15 months the reduction was 99 per cent. The higher dosage was applied earlier in the year and 6·67 inches of rain fell between its application and subsequent sampling when it gave 43 per cent. reduction, which improved to 83 per cent. after the additional 34·38 inches of rain.

Discussion.

The most interesting fact that emerges from these field trials is the prolonged persistence of insecticides in peat. Most of them (DDT, dieldrin, chlordane) were not merely just as effective three years after application as they were after one year but were even more effective with the passage of time. This persistence will help to compensate for the initial delay that occurs between the application of an insecticide and the attainment of adequate control. It will also facilitate the adoption of larval control methods by interested persons because the cost can be spread over a number of years. The present evidence is that the control will continue to be effective for at least three years and probably much longer as there is no sign of loss of efficiency except with γ BHC.

Summary.

This paper presents further observations on the continued persistence of larvicidal treatments applied to small plots (10 yd. × 10 yd.) on Soutra Hill, Midlothian, to control larvae of the biting midge, *Culicoides impunctatus* Goetgh. Before doing so, consideration is given to the nature of the observed fluctuations in larval population encountered in the untreated plots. Evidence is produced which indicates that this is not due either to delayed hatching of eggs (this, if it occurs, is of minor importance), to change in technique or to the application of insecticide to neighbouring plots, but is due to the larvae responding to an oscillating factor (or factors) in the breeding site. It is suggested that one such factor might be soil water level. Therefore, it follows that changes in the untreated larval population must be taken into account when assessing the degree of control achieved by treatments, especially when the larval population is declining.

As regards insecticidal persistence three years after application:—

(i) Nine of the eleven DDT treatments (wettable powder, water-miscible concentrate and dust at 12, 50 and 200 mg. p,p′DDT/sq. ft.) gave 100 per cent. control. The other two (both wettable powder at 12 mg./sq. ft.) produced 75 and 22 per cent. reduction.

(ii) Only one of seven γ BHC treatments (wettable powder at 50 mg. γ BHC/sq. ft.) gave complete control and one treatment (w.p. 12 mg./sq. ft.) was completely ineffective.

(iii) DDT retained its superiority to γ BHC as a larvicide against *Culicoides*, achieving 93 per cent. control compared with 55 per cent. for γ BHC.

(iv) The lowest dosages of dieldrin (3 mg./sq. ft.) and chlordane (6 mg./sq. ft.) had begun to lose their larvicidal power, control declining from 76 to 53 per cent. and 67 to 29 per cent., respectively. There was no change at 6 mg. dieldrin/sq. ft. but the other treatments (12 and 25 mg. dieldrin and 12, 25 and 50 mg. chlordane/sq. ft.) had improved. Dieldrin at 12 and 25 mg./sq. ft. and chlordane at 50 mg./sq. ft. attained complete control.

The spray-volume treatments, now in their second year, showed an increase in activity. This was most marked in the wettable-powder treatments at 25 mg. p,p′DDT/sq. ft. which a year ago were completely ineffective and now five out of six trials gave complete control and the other 97 per cent. Improvement in the treatments at 50 mg./sq. ft. was less (from 43 to 83%) due in the main to the complete failure of one treatment (10 gal./acre).

It is confirmed that spray volume in itself is unimportant in larvicidal applications providing the coverage is adequate.

Acknowledgements.

We wish to record our continued thanks to the Scottish Tourist Board for financing this work and to Professor M. M. Swann for giving us every facility in his department.

References.

Hill, M. A. (1947). The life-cycle and habits of *Culicoides impunctatus* Goetghebuer and *Culicoides obsoletus* Meigen, together with some observations on the life-cycle of *Culicoides odibilis* Austen, *Culicoides pallidicornis* Kieffer, *Culicoides cubitalis* Edwards and *Culicoides chiopterus* Meigen.—*Ann. trop. Med. Parasit.* **41** pp. 55–115.

Kennedy, J. S. (1947). The excitant and repellent effects on mosquitos of sublethal contacts with DDT.—*Bull. ent. Res.* **37** pp. 593–607.

Kettle, D. S. & Lawson, J. W. H. (1952). The early stages of British biting midges *Culicoides* Latreille (Diptera: Ceratopogonidae) and allied genera.—*Bull. ent. Res.* **43** pp. 421–467.

Kettle, D. S., Nash, R. H. & Hopkins, B. A. (1956). Field tests with larvicides against *Culicoides impunctatus* Goetgh. in Scotland.—*Bull. ent. Res.* **47** pp. 553–573.

Kettle, D. S. & Parish, R. H. (1957). Field trials of larvicides against *Culicoides* with a discussion on the relationship between rainfall and larval control.—*Bull. ent. Res.* **48** pp. 425–434.

Parker, A. H. (1950). Studies on the eggs of certain biting midges (*Culicoides* Latreille) occurring in Scotland.—*Proc. R. ent. Soc. Lond.* (A) **25** pp. 43–52.

© Commonwealth Agricultural Bureaux, 1959.

THREE NEW STRAINS OF *AMPHOROPHORA RUBI* (KALT.) ON CULTIVATED RASPBERRIES IN ENGLAND.

By J. B. Briggs
East Malling Research Station.

In various experiments during the last 20 years, different stocks of *Amphorophora rubi* (Kalt.) have fed on different plants or on different ranges of plants, and the workers concerned have concluded that the species should be sub-divided into strains or even new species. Thus Börner (1939) was unable to transfer one form from bramble to raspberry, or another form from raspberry to bramble. In a later paper (1952) Börner described the food-plants of the first form as "*Rubus caesius* and vigorous species", and the food-plant of the latter form as "*Rubus idaeus*, but not living on true (*eigentlich*) *Rubus* species". On the basis of this result, together with certain morphological differences, he sub-divided the species into two, giving the name *Nectarosiphon rubi* (Kalt.) to the form breeding on *R. caesius*, and proposing the name *Nectarosiphon idaei* Börner for the raspberry form. Hille Ris Lambers (1949) examined more material and rejected the morphological evidence given by Börner, and sank Börner's two species in *Amphorophora rubi* (Kalt.).

Schwartze & Huber (1937) reported from western Washington, U.S.A., that the raspberry variety Lloyd George had never been found infested in many field counts, nor were aphids able to maintain themselves on this variety in the greenhouse. Dicker (1940) found as many as 130 aphids per cane in England, and concluded that two forms of *A. rubi* existed, one in North America and one in England. He considered their morphological similarity made it unlikely that species existed and suggested that they should be described as strains. Hill (1956) working at Vancouver with plants raised from root cuttings sent from Great Britain, provided evidence that aphids collected locally could not colonise Lloyd George or Malling Promise but would colonise Malling Landmark.

Thus at the start of the present work three strains were recognised: Börner's *R. caesius* strain, which he considered a true species, intolerant of *R. idaeus*; the North American strain from raspberry, intolerant of the variety Lloyd George; and the European raspberry form, breeding on Lloyd George. Recent work at East Malling by R. L. Knight, E. Keep & J. B. Briggs (to be published in the *Journal of Genetics*) connected with plant breeding for resistance to *Amphorophora rubi* indicated that the European raspberry form itself existed in three different forms, and experimental work by the present author has shown that these forms behave so consistently that they should be recognised as strains.

Evidence for the Existence of new Strains.

In describing the reaction of the various strains of aphid to different varieties of the food-plant it is necessary to refer to many un-named seedling selections as well as to named varieties. For the sake of simplicity these are described beforehand with an indication of their relationships to one another.

Rubus idaeus—Red raspberry varieties.

Lloyd George, a commercial raspberry variety; Malling Promise, a commercial raspberry variety raised at East Malling; P1, a basic parent line of raspberry described by Knight, Keep & Briggs (*loc. cit.*); Chief, a commercial American raspberry variety; 87/6, a selection from a family of the parentage Chief selfed;

TABLE I.

Reaction of raspberry varieties and selections to aphids of strains 1–3.

Variety or selection	Strain 1		Strain 2		Strain 3	
	Total no. of tests	Reaction	Total no. of tests	Reaction	Total no. of tests	Reaction
Malling Promise	1	+	1	+	2	+
P1	1	+	2	+	2	+
Chief and derivatives						
Chief	1	o	—		—	
87/6	11	o	6	o	3	+/o
87/6 derivatives (52 seedlings) ..	1 each	all o	—		1 each	all +
Baumforth A and derivatives						
Baumforth A	7	o	2	+	—	
Malling Landmark	9	o	4	+	3	o
Baumforth A derivatives (32 seedlings)	1 each	all o	1 each	all +	—	

87/6 derivatives, seedlings deriving from crosses and back-crosses between 87/6 and P1; Baumforth A, an obsolete raspberry variety of unknown origin; Malling Landmark, a raspberry variety of the parentage Preussen × Baumforth A; 64/2, a selection from a family of the parentage Landmark × P1; Baumforth A derivatives, seedlings of the parentage Landmark selfed, or Baumforth A × P1; September, a commercial American variety.

Rubus caesius.

John Innes blackberry, *Rubus rusticanus inermis* × *Rubus thyrsiger.*

Amphorophora rubi: Raspberry strain 1.

In 1952, aphids were collected from mixed raspberry varieties at East Malling. Aphids reared from these were used from 1952 to 1954, when a further collection was made at East Malling from the variety Malling Promise; the reared progeny of these aphids were used from 1955 to 1957. These two reared lines were used to test a wide range of varieties and selections, growing in pots in an insectary, as sources of resistance. Clear-cut and reproducible results were obtained which showed that the plant range of the two reared lines was the same. When, however, departures from this pattern of plant reaction were later found in other stocks of aphids, the form that had been used in these tests was designated strain 1, other forms described later in this paper being designated strains 2 and 3. The reaction of many varieties to strain 1 are reported by Knight, Keep & Briggs (*loc. cit.*) and are in general agreement with the findings of Hill (1957), who was presumably working with a similar form. The reaction of varieties and selections relevant to the present discussion are listed in Table I, where " + " denotes complete susceptibility, and " o " denotes resistance, no breeding of aphids having been observed in any test after repeated heavy inoculations with both winged and wingless summer forms. The symbol " + /o " denotes a reaction intermediate between the preceding two described.

Amphorophora rubi: Raspberry strain 2.

Knight, Keep & Briggs (*loc. cit.*), in the plant breeding work mentioned, compared populations of *A. rubi* in plantations over a wide area, on Malling Landmark or 64/2, with those on a standard susceptible variety, usually Malling Promise. Differences were normally very striking, but at one locality, Ryarsh in Kent, the population on Landmark was higher than usual, and aphids were collected from this variety for study. When transferred to potted plants of Landmark in an insectary these aphids settled down and commenced to feed, and have subsequently been reared through many generations on this variety. The reaction of Landmark and other varieties to this form is shown in Table I; comparison with strain 1 shows that whereas Baumforth A and its derivatives that were used are resistant to strain 1, they are susceptible to this form, which was accordingly considered a separate strain and named strain 2.

Amphorophora rubi: Raspberry strain 3.

In 1955, Knight, Keep & Briggs (unpublished) planted in the field at East Malling derivatives of 87/6, shown by insectary test to carry the resistance of the parent to aphids of strain 1; they quickly became infested with aphids. It was not then appreciated that the aphids responsible differed from those used in the insectary; it was thought that some change in the plants was responsible for their loss of resistance. Further derivatives of the next generation were tested in the insectary in 1957, and large numbers of plants again showed resistance to aphids of strain 1. When, however, due to a temporary shortage of aphids and an

accumulation of plants, aphids from the field were used to test similar plants in another insectary, the number of resistant plants fell below expectation, increasingly so as aphids reared from those collected in the field were used. Examination of the records showed that many plants were colonised by aphids derived from a single progenitor. When a stock of aphids derived from this single female was isolated and used for further testing, nearly all 87/6 derivatives under test were colonised; the aphids were apparently of a third type. The reaction of this stock of aphids to the parent variety 87/6 was not quite so successful, however; nearly as many aphids walked off the plant as settled and commenced to reproduce. The reaction of various varieties to this form is shown in Table I. Whereas 87/6 and those of its derivatives that were tested were completely resistant to strains 1 and 2 they were susceptible to this form, fully so except in the case of 87/6 itself, discussed above. Landmark and other Baumforth A derivatives had been shown to be resistant to strain 1 but susceptible to strain 2; Landmark itself was resistant to this last form. In view of these differences this form was, therefore, distinguished as strain 3.

Comparative Behaviour of the three Strains under uniform Conditions.

In 1957, each of the three strains was tested simultaneously in a separate insectary compartment containing single potted plants of each of three critical varieties. These were dipped in nicotine, thoroughly inspected, and after a short interval isolated by standing the pots on empty inverted pots in a tray of water. This ensured that there were no stray aphids present before the test and reduced plant to plant movement during the test to a minimum. Each plant was then inoculated with ten apterae; if these failed to become established, larger numbers were added. After sufficient aphids had been added to show the differences clearly, inoculation was discontinued, and the aphids on the plants counted 14 days later. The results are shown in Table II; each resistant variety was free from aphids of the strains to which it had been shown (Table I) to be resistant, despite large inoculations, whereas the populations in the other combinations of variety and strain had risen markedly from the first inoculation. This effect was less marked with the "intermediate" 87/6, which required an inoculation with a total of 20 aphids of strain 3 before any aphids settled, a procedure which was followed with the Promise plant inoculated with strain 3 for purposes of comparison.

TABLE II.

Population of aphids of three strains on plants of raspberry varieties 14 days after last inoculation.

Variety	Strain 1		Strain 2		Strain 3	
	Inoculation	Progeny	Inoculation	Progeny	Inoculation	Progeny
Promise	10	74	10	106	20	111
Landmark ..	140	0	10	141	100	0
87/6	140	0	410	0	20	47*

* After 34 days.

Distribution and Abundance of the Strains.

Since the identification of these strains is dependent on host reaction, it has been possible to obtain much more information on the distribution of strain 2, by inspecting plantations of Landmark, which is still grown in some areas, than that of strain 3, since varieties of the type of Chief and 87/6 are not grown in this country. The presence of strain 3 at East Malling, is, of course, known, due to the circumstances of its discovery; moreover the general breakdown of 87/6 derivatives planted out in 1955, mentioned earlier, suggests very strongly that it was present then, and moreover that it was abundant. No information is available as to whether the generally distributed form elsewhere is strain 1 or 3. The distribution of strain 2 is better understood. Small foci of infestation have been found on Landmark at Beccles, Suffolk, and in three separate areas of the breeding plot at East Malling on various Landmark derivatives. In these cases, aphids were collected and bred on Landmark in the insectary. Similar foci of infestation were observed at Yalding and Brogdale in Kent. The numbers of aphids on Landmark and its derivatives have always been a small proportion of those found on Promise, in all the counts made, with the exception of the ones at Ryarsh, but where aphids have been found they have occurred in aggregations suggesting spread from a point source. In the case of the breeding plot at East Malling, where no aphicidal sprays are used, these aggregations have recurred in most cases in the same spot in successive years. Here, at least, opportunity for general spread should have existed. Since the value of plant breeding for resistance to *A. rubi* from the Baumforth A source would be greatly reduced if strain 2 were to become generally distributed and abundant, as much information as possible has been gathered on the bionomics of this strain.

Counts were made of aphid populations on Landmark and Promise on the plot at Ryarsh, which consists of approximately equal halves of each variety. One count was made in 1955; aphids were not abundant enough in 1956 to be worth counting, but in 1957, six counts were made. The results are shown in Table III. Except when the population was low and sampling error great, the population was always lower on Landmark than on Promise, and, since there are about five times as many spawn growths on Promise as on Landmark, the differences shown

TABLE III.

Number of aphids of all stages present on spawn of Promise and Landmark at Ryarsh, Kent.

Date of count	No. of leaves or canes examined	Total no. of aphids		Percentage of sample leaves or canes infested	
		Landmark	Promise	Landmark	Promise
8.vii.55	115 leaves	361	638	?	?
14.v.57	100 ,,	45	1004	5	68
23.v.57	100 ,,	320	3282	28	94
7.vi.57	200 ,,	132	643	21	70
21.vi.57	200 ,,	88	603	25	74
1.vii.57	200 ,,	26	171	11	44
22.viii.57	50 canes	32	23	18	32

are probably underestimated. The percentage of infested leaves or canes of Landmark never rose above 28 per cent., whereas at the same time virtually all the Promise samples were infested (Table III, 23rd May 1957); further searching showed that unattacked *stools* of Landmark could be found, whereas no *cane* of Promise examined was free of aphids. The rate of increase of the populations on

the two varieties was similar, as was the ratio of adults/nymphs, a good index of population growth. It thus seems that the differences in population level were not due to extraneous factors such as differential levels of predation or rate of reproduction, since these would surely be reflected in the adult/nymph ratios, but to a different basic level of population early in the season. The aphids breeding on Landmark were of strain 2, but those on Promise were shown to be of one of the other strains; of 128 adult aphids transferred from Promise to potted plants of Landmark in the insectary, none survived. The figures for the populations on the two varieties at Ryarsh may therefore be considered as a measure of the populations of the two strains. Coupled with the observation made elsewhere that infestations of strain 2 are restricted to foci, although there is no apparent barrier to its spread during the summer months, the evidence suggests that there is some special mortality factor operating against this strain during the colder months of the year, the ground gained in spread one year being largely lost and foci in the following year arising in the same spot, from a small number of survivors.

Other Strains on Raspberry and Blackberry.

Other experiments were necessary to establish that the three strains described were not identical with Börner's *R. caesius* strain or the North American strain described in the introduction. Since Börner did not name the variety of *Rubus idaeus* with which he was working, the three strains were tested on *Rubus caesius* itself; all failed to breed, as they did on John Innes blackberry. Aphids of all three strains bred successfully on Lloyd George. There seems no doubt that the three new strains described are distinct from either the *R. caesius* strain or the North American strain.

One other discrepancy in observed and reported behaviour of *A. rubi* suggests the existence of yet another form. Kronenberg & de Fluiter (1951) state that in Holland the variety September [1] is resistant to *A. rubi*, but in the present author's experiments this variety was readily colonised by strains 1, 2 and 3. Should the variety September be found to be consistently resistant in Holland, this would indicate the existence of yet another strain.

Discussion.

While sufficient material has not yet been collected from the field to make a detailed morphological examination of all stages in the life-history of the three strains, examination of many reared apterae does not suggest that specific or subspecific status should be considered for these forms. It is suggested that the following nomenclature should be used in referring to these strains.

Amphorophora rubi (Kalt.)

Rubus caesius strain
North American strain
European raspberry strain 1
European raspberry strain 2
European raspberry strain 3

The economic importance of these strains is related to the use of raspberry varieties bred for resistance to *A. rubi*. So long as susceptible plants are grown, and reliance is placed on other methods to combat the spread of the viruses of which *A. rubi* is the vector, the question of which strain is present is not important, assuming that they are all of equal potentiality as virus vectors.

[1] In the paper by Kronenberg & de Fluiter, the variety here called September is referred to as Milton, but it is in fact September (Personal communication by Dr. Kronenberg).

But if, as in the case of the plant breeding programme at East Malling, it is proposed to produce varieties resistant to *A. rubi*, then a knowledge of all the strains involved and the range of plant varieties on which they feed is essential to the production of full resistance. This aspect is further discussed by Knight, Keep & Briggs (*loc. cit.*) in connection with strain 2. Since the success of the plant breeding programme may ultimately be related to the ability of the insect to produce further variants, further work is planned to attempt to achieve an understanding of the origin of these newly discovered strains.

Summary.

Previous work on strains of *Amphorophora rubi* (Kalt.) is discussed and evidence is presented to show that the form on European raspberry can be divided into three strains. These are designated European raspberry strain 1, 2 and 3. The distribution, abundance and importance of the strains in relation to plant breeding for resistance to *A. rubi* is discussed.

Acknowledgements.

The author wishes to thank his colleagues, Dr. R. L. Knight and Miss Elizabeth Keep, for their help, notably with the provision of plant material.

References.

Börner, C. (1939). Neue Gattungen und Arten der mitteleuropäischen Aphidenfauna.—*Arb. physiol. angew. Ent. Berl.* **6** pp. 75–83.

Börner, C. (1952). Europae centralis aphides. Die Blattläuse Mitteleuropas: Namen, Synonyme, Wirtspflanzen, Generationszyklen.—*Schr. Thüring. LandArbGemeinsch. Heilpflanzenk. Weimar* Heft 4, 1. Lief. (*Mitt. Thüring. bot. Ges.* Beih. 3, 1. Lief.) 260 pp.

Dicker, G. H. L. (1940). The biology of the *Rubus* aphides.—*J. Pomol.* **18** pp. 1–33.

Hill, A. R. (1956). Observations on the North American form of *Amphorophora rubi* (Kalt.) (Homoptera, Aphididae).—*Canad. Ent.* **88** pp. 89–91.

Hill, A. R. (1957). Observations on the reproductive behaviour of *Amphorophora rubi* (Kalt.), with special reference to the phenomenon of insect resistance in raspberries.—*Bull. ent. Res.* **48** pp. 467–476.

Hille Ris Lambers, D. (1949). Contributions to a monograph of the Aphididae of Europe. IV.—*Temminckia* **8** pp. 182–323.

Kronenberg, H. G. & de Fluiter, H. J. (1951). Resistentie van frambozen tegen de grote frambozenluis *Amphorophora rubi* Kalt.—*Tijdschr. PlZiekt.* **57** pp. 114–123.

Schwartze, C. D. & Huber, G. A. (1937). Aphis resistance in breeding mosaic-escaping red raspberries.—*Science* **86** no. 2224 pp. 158–159.

© Commonwealth Agricultural Bureaux, 1959.

FUNGOUS DISEASES OF LAMELLICORN LARVAE IN SOUTHERN RHODESIA.

By G. H. Bünzli * and W. W. Büttiker.*

In the course of a study of the biology of the white grubs occurring in tobacco fields in Southern Rhodesia, the opportunity was taken to record the natural enemies of the two most important species, *Anomala exitialis* Pér. (Rutelinae) and *Schizonycha profuga* Pér. (Melolonthinae), each with a one-year life-cycle. Insects that are predacious and parasitic on these larvae have been listed in previous papers (Bünzli & Büttiker, 1956, 1957*a*,*b*).

Entomophagous micro-organisms forming part of the complex of natural enemies of the larvae readily escape attention because their action in epidemic form is rare and very localised. In order to ascertain the pathogens involved and throw light on their erratic incidence, investigations were carried out on soil and insect samples collected on Dunstan Farm, Melford District, Southern Rhodesia.

Occurrence of a Disease.

On 19th December 1950, random digging in a field led to the discovery of a rather small area in which some of the white grubs exhibited symptoms of a mild disease in the form of dark spots on the integument. The percentage of specimens thus affected varied according to the density of the population from 5 to 36 per cent., the latter percentage coinciding with the unusually high number of 24 grubs per sq. yd. Unfortunately, larvae so affected, when preserved in alcohol and examined later, proved to be unsuitable for study.

Observations in the same area were resumed in January 1952, in the hope that the pathogen in one stage or another would have survived in the soil and attacked the new white-grub population. In the 1951/52 season, maize had succeeded the tobacco crop of 1950/51. The larvae were far less abundant and more irregularly distributed, averaging 3–4 individuals per sq. yd. and thus more extensive digging was necessary. The larval population consisted on an average of 76 per cent. *A. exitialis* and *S. profuga*, 18 per cent. of various smaller *Anomala* species and 6 per cent. of two *Serica* species. As in the previous year, only larvae of the first two species were found to be susceptible to disease; accordingly the following field records taken in January to March refer to this group of larvae.

Variation of frequency of affected larvae and progress of disease (1952).

Date of collection	7.i	30.i	19.ii	1.iii	15.iii
Number of white grubs	51	33	41	130	80
„ „ „ „ infected, alive ..	21	11	8	96	34
„ „ „ „ „ dead ..	—	—	—	6	23
Percentage diseased	41	33	20	78	71

* Formerly of the Research Staff of the Tobacco Pest Control Research Scheme, Salisbury (Southern Rhodesia).

Due to the uneven distribution of the white grubs and the sources of infection within the ill-defined area, the rates of diseased larvae collected on consecutive dates lack uniformity and regular progression. The first casualties occurred towards the end of February (4·61%) and by the middle of March the number of grubs that had succumbed rose to 28·75 per cent.

The percentages of infected grubs, however, refer to visibly affected specimens only and represent minima. Apparently healthy larvae of the two last collections were kept in the laboratory under individual observation until the end of April. As expected, some of them developed the characteristic symptoms of the disease so that the final percentage of infected larvae rose to 95 and 82, respectively. The disease actually had acquired an epidemic character.

On 30th January 1952 the adjacent field (under fallow) was surveyed. The larval infestation was light and consisted of 69 per cent. *A. exitialis* and *S. profuga*, 24 per cent. various small RUTELINAE and 7 per cent. TENEBRIONIDAE (*Psammodes scrobicollis* (Fhs.) and *P. similis* Pér.). No signs of pathogenic disturbances were noticeable. On re-inspecting the same field on 28th March, 3 per cent. of the first group of insects were found to be affected. It is most probable that similar low rates of infection prevail throughout the tobacco-producing districts towards the end of the growing season but contribute little to a reduction of the survival potential of this economically important pest.

The Pathogens involved.

Definitely diseased white grubs were dried in the incubator at 25°C. and representative specimens of three groups of fungi were sent to the Commonwealth Mycological Institute, Kew, Surrey, for identification.

Torrubiella sp. (Hypocreales).

This fungus proved to be by far the most prevalent pathogen. According to Petch (1923) the taxonomy of this fungus is difficult because " Barren stromata of *Torrubiella* are most annoyingly common ". These stromatic (sclerotioid) spots, brown to black in colour and one to six per individual grub, are irregularly spread all over the integument. They vary in size but the head capsule and the spiracles are free of diseased areas. Blackening of the region of the spiracles is associated with a bacterial disease of *Lachnosterna* spp. caused by *Micrococcus nigrofaciens* Northrup (Northrup, 1914). Larvae of *Anomala exitialis* and *Schizonycha profuga* infected with *Torrubiella* that were collected between December and February did not appear to be markedly inconvenienced by the action of the slow-growing mycelia since they moved and fed normally in the soil. Laboratory tests, however, revealed that 80 per cent. of the visibly infected *Anomala* larvae dug up on the 30.i.1952, and 50 per cent. of those collected on the 19.ii.1952, succumbed by mid-April. Individual black areas on the integument became irregularly enlarged and those originally located close together fused to form elongated patches. Short, white, aerial filaments sometimes bordered the discoloured regions. In the case of *Schizonycha*, which reaches the adult stage in March–April (*Anomala* hibernates as a fully fed larva), the process of moulting, including that of pupation, is seriously disturbed by the presence and growth of the fungus. At these critical stages, when part of the old cuticle is resorbed and the hypodermis produces a new chitinous coat, the diseased areas do not conform, with the result that constrictions and other malformations develop in the third-instar larvae, pupae and/or young adults. Such individuals die gradually in the laboratory but under field conditions they succumb rapidly to one of the muscardine fungi (see below) which envelop the insect in a web of hyphae. This incidence of secondary, more active and spectacular fungi is apt to veil the primary *Torrubiella* infection and probably may account for the absence of any records of Scarabaeid larvae being attacked by this pathogen. Petch (1944) states:

" Entomogenous fungi from the tropics, if not dried rapidly, are soon over-run by *Aspergillus* and *Penicillium* ".

All the known species of the genus *Torrubiella* (Boudier) are entomophagous (Petch, 1923): ten occur on Coccids and Aleyrodids, 4 on Lepidoptera, 7 on Arachnids, 1 on Diptera and 1 on Chrysopids (Petch, 1937, 1944). Three species occur in Britain.

The species of the allied genus *Cordyceps* (Fr.) Link, also are mostly entomophagous. *C. entomorrhiza* Dicks. attacks larvae of *Melolontha melolontha* (L.) and *Amphimallon solstitiale* (L.) (cited as *Rhizotrogus*) in France (Giard, 1891*b*), *C. melolonthae* (Tul.) Sacc., those of *Lachnosterna fusca* (Froel.) (Giard, 1891*a*), *C. ravenelii* Berk., *Lachnosterna* (cited as *Phyllophaga*) in U.S.A. (Davis, 1919), *C. barnesii* Thwaites, Melolonthine grubs in Ceylon (Petch, 1924). *C. myrmecophila* Cesati is known to parasitise the widely spread African Ponerine ant, *Paltothyreus tarsatus* (F.) (Bequaert, 1922), and it has also been observed to do so in Southern Rhodesia. This earth-dwelling ant, which does not climb plants in order to hunt insects, was occasionally found parasitised, fixed by the mandibles to grass haulms and with slender stromata growing out of the body.

Beauveria (*Botrytis*) *bassiana* (Bals.) Vuill. (Moniliales).

This fungus was found to be of secondary importance in controlling white grubs in nature, but under abnormally wet weather conditions it appears that the common Rhodesian field cricket, *Brachytrupes membranaceus* (Dru.), is very susceptible to attack by it. The mycelium rapidly penetrates the body of infected white grubs and therefore causes premature death, much swifter than in the case of *Torrubiella*, which thrives mainly in the hypodermis. Five of the 23 dead grubs collected on 15.iii.1952 developed *Beauveria bassiana* in a short time, when kept separately in glass tubes, the cottony masses of hyaline hyphae with conidial heads completely concealing the insect body. Under natural conditions within the soil the fungus always appears to produce a chalky layer on the integument of the host.

Almost cosmopolitan, *B. bassiana* is pleophagous and attacks many insects of various families. In North America it is known from 30 and its congener *B.* (*Sporotrichum*) *densa* (Link) Vuill. from 70 different species (Charles, 1941). *B. densa* is a pest of the silkworm, *Bombyx mori* (L.).

In South Africa, *B. bassiana* sometimes attacks *Nomadacris septemfasciata* (Serv.), but only if the general health of the locust populations is impaired (Schaefer, 1937). According to Dr. J. C. F. Hopkins (private communication, 1958), Wickens also recorded this fungus on the same host in Southern Rhodesia about 1934. In Europe, Giard (1891*a*) mentions the finding of larvae and Delacroix (1893) imagines of *Melolontha melolontha* diseased by *Beauveria* (*Botrytis*, *Isaria*) *bassiana*. Giard (1893) successfully infected larvae of *Anomala dubia frischii* (F.) and *Polyphylla fullo* (L.) with *B.* (*Isaria*) *densa*, the pink muscardine, originally isolated from cockchafers; Prillieux & Delacroix (1891) infected, with the same fungus, larvae of *Cetonia aurata* (L.) and *Amphimallon solstitiale*. Moutia (1940) in Morocco recorded *B. bassiana* as well as *B. densa* on larvae of *Rhizotrogus carduorum* Erichs. and *Amphimallon semivillosum* (Fairm.). Rex (1940) obtained 100 per cent. infection in adults of *Popillia japonica* Newm. dusted with spores of *B. bassiana*; feeding on leaves sprayed with an aqueous solution of spores also produced infection.

Metarrhizium anisopliae (Metsch.) Sorokin (Moniliales).

This green muscardine fungus developed in the laboratory on a few specimens only of apparently healthy white grubs collected during February–March. Its occurrence as a primary pathogen is rather sporadic and it was confined to *Anomala exitialis* which passes the dry winter months in the subsoil as a full-fed

third-instar larva. The hyphae penetrate the entire lumen of the body and death rapidly ensues, although in the early stages it is difficult to recognise the disease. After the grub has succumbed, the rigid body becomes mummified and is enveloped with a white hyphal down, the branching mycelia producing the sporophores. The ripe conidial stage is characterised by a comprehensive olive green-greyish cover of spores which develops rather rapidly.

The fungus was discovered by Metschnikoff (1879) on the Ruteline, *Anisoplia austriaca* (Hbst.), a small European cockchafer injurious to various cereals. This author—the first who seriously investigated the possibilities of controlling insects by fungi—used it against *Anisoplia* and the Curculionid, *Cleonus punctiventris* (Germ.), which is harmful to sugar-beet in southern Russia.

Metarrhizium anisopliae occurs practically all over the world and attacks many insects above and in the soil. In humid warm climates the pathogen is parasitic mainly on Lamellicorn grubs, of such species as *Xylotrupes* (now *Dynastes*) *gideon* (L.), but occasionally also on Cerambycids with earthbound larvae, and on locusts, etc. Dammerman (1929) states that, in south-east Asia, *M. anisopliae* attacks *Adoretus compressus* (Weber), a defoliator of cacao, coffee, banana, kapok, sugar-cane, etc., both in the larval and adult stages. Pemberton (1939) recorded it on *Anomala orientalis* Waterh., a root pest of pineapple and sugar-cane in Hawaii, and Moutia (1940) on species of the Melolonthine genera *Rhizotrogus* and *Amphimallon* in Morocco. Rockwood (1951) found *M. brunneum* Petch naturally controlling the wireworm, *Limonius californicus* (Mannh.) in Oregon.

Among various attempts made to culture and use *M. anisopliae* for biological-control purposes the following may be mentioned: Pettit (1895) and Davis (1919) against larvae of *Lachnosterna* (cited as *Phyllophaga*) in the U.S.A., Rorer (1910) against the leafhopper, *Saccharosydne* (cited as *Delphax*) *saccharivora* (Westw.); Urich (1913), Rorer (1913), Pickles (1933) against the froghoppers, *Aeneolamia* (cited as *Tomaspis*) *varia* (F.) and *A.* (*T.*) *saccharina* (Dist.) on sugar-cane in Trinidad and Tobago; Stevenson (1916) against white grubs in Porto Rico; Friederichs (1913) against the coconut beetle, *Oryctes rhinoceros* (L.), in Samoa; Wallengren (1930) and Hergula (1930) against the European corn borer, *Pyrausta nubilalis* (Hb.).

In Rhodesia, with a semi-arid climate, the prospects of using any one of the three entomophagous fungi recorded on white grubs for the control of pest species of Melolonthids appear to be very slender (see below). Of *Cordyceps entomorrhiza*, Sweetman (1936) states: "the efficacy of artificially propagating the fungus to control Scarabaeid larvae has not been established definitely and no method of doing so can be recommended at present."

Ecology of the Fungi.

Torrubiella alone or occasionally in conjunction with *Beauveria* and *Metarrhizium* have been found to attain the level of an epidemic disease in *Anomala exitialis* and *Schizonycha profuga* only under exceptional circumstances. Although it appears that entomophagous fungi are ubiquitous in the light tobacco soils of Southern Rhodesia, the remarkable decimation of the white grubs recorded above was restricted to a single very localised site.

The pedological conditions most favourable for the development of white grubs when unaffected by pathogens have been specified. The occurrence of abundant populations of *A. exitialis* and *S. profuga* larvae is correlated with feeding grounds which are relatively well provided with nitrogenous organic matter.*

The data obtained from partial mechano-chemical analysis of top-soil samples taken to the depth of 25 cm. from the area containing diseased white grubs

* According to Giard (1891*a*), white grubs contain about 3·1 per cent. total nitrogen.

(2 records) are compared, in Table I, with those from sites in which the white grubs were healthy (12 records).

It emerges that the two substrata, though very uniform, do, however, differ very markedly in the humus-nitrogen complex. The erratic high amount of organic matter in (A) virtually satisfies the food requirements for the development

TABLE I.

Partial mechano-chemical analysis, per cent., of samples of soils that had contained, respectively, fungus-infected and healthy white grubs.

Fraction or constituent	Soil samples	
	(A) Fungus-infected	(B) Normal
Gravel (2–10 mm.) %	11·0 (8·4–13·6)	12·25 (4·2–26·7)
Fine earth (2 mm.) 100%		
Sand (coarse and fine) % ..	82·5 (81·7–83·3)	82·5 (80·2–83·7)
Silt %	11·3 (10·5–12·1)	11·02 (9·6–13·0)
Clay %	6·2 (6·2–6·2)	6·48 (6·2–6·8)
Hygroscopic moisture	1·02 (0·77–1·27)	1·08 (0·53–2·60)
Loss on ignition	5·23 (4·27–6·20)	3·65 (2·37–5·07)
Nitrogen	0·140 (0·130–0·150)	0·082 (0·067–0·103)
Humus (N × 20)	2·80 (2·60–3·00)**	1·64 (1·34–2·08)

of a very dense population of white grubs, but on the other hand coincides with conditions apparently favourable for the survival of virulent pathogens, and is inducive to the development of particularly aggressive strains.

In Rhodesia, where high-grade Virginia tobacco is being grown, comprehensive areas with a naturally high fertility status do not occur; small patches, which are not linked with any particular topographical feature, representing places where mould derived from the fallen leaves of clumps of trees has been preserved and ploughed in, are favourable for supporting dense populations of white grubs. The very locality which has proved to be severely infected with entomophagous fungi was confined to the edge of a field, bordered by large native trees, the substratum contrasting with the bulk of the adjacent arable soil by its definitely darker colour. The residual organic matter imparts a better soil structure and thus enhances its capacity for water retention. During the peak activity of the white grubs the humidity is more balanced. These conditions appear to be more favourable to the viable stages of the fungi attacking the white grubs, which, in presence of ample food, do not require to move much in any direction. On the other hand, the drying-up of the soil to a considerable depth during the cool and rainless winter period is most likely favourable to the survival of the pathogen.

Little information is available concerning the ecology of entomophagous fungi in the soil. Pyatnitzkiĭ (1940) states that *Metarrhizium anisopliae* is found in Russia more on acid-reacting soils, whereas *Tarichium uvella* Krass. (*Empusa*, *fide* Fitzpatrick, 1930) favours more alkaline substrata. Meĭer (1940) concludes

** In compost and manure heaps the common field Melolonthids, *Anomala* and *Schizonycha*, are replaced by true dung beetles.

that fungous diseases among soil pests may follow a change in acidity of the soil effected by suitable manures.

The pH of many Rhodesian soils investigated that contained white grubs was found to vary between 4·5 and 6·5; the area containing diseased larvae showed values varying between 5·5 and 6·0. The conditions which control the transition from the saprophytic to the parasitic behaviour (and *vice versa*) of soil fungi which assume an entomophagous character are obscure. Propagation in the soil over a distance by hyphae appears to be possible only if there is sufficient humus in the soil.

Summary.

One exceptional instance of a mycosis, with epidemic character, in white grubs has been studied in Southern Rhodesia.

The hosts were the larvae of *Anomala exitialis* Pér. and *Schizonycha profuga* Pér., which are tobacco pests, the entomophagous fungi being *Torrubiella* sp. (most prevalent), *Beauveria bassiana* (Bals.) Vuill. and *Metarrhizium anisopliae* (Metsch.) Sorokin.

Soil with an abnormally high content of nitrogenous organic matter favours the breeding of the two insects but at the same time provides a suitable medium for the survival and development of a high degree of virulence in the cryptogamic pathogens.

Acknowledgements.

We owe grateful thanks to Professor Dr. E. A. Steinhaus, University of California (Berkeley) who was kind enough to ascertain that bacteria could hardly be considered as primary pathogens in specimens of white grubs sent for examination. We express our sincere appreciation of the interest taken by Dr. S. P. Wiltshire and Major H. A. Dade of the Commonwealth Mycological Institute, Kew, Surrey, who willingly accepted collections of infected insects. The taxonomic work was done by Dr. M. B. Ellis, of the above Institute, to whom we are particularly obliged for the microscopical investigations carried out on our behalf.

References.

Bequaert, J. (1922). The predacious enemies of ants.—*Bull. Amer. Mus. nat. Hist.* **45** pp. 271–331.

Bünzli, G. H. & Büttiker, W. W. (1956). Insects in Southern Rhodesian tobacco culture. Part I. Insects occurring in seed-beds.—*Acta trop.* **13** pp. 352–365.

Bünzli, G. H. & Büttiker, W. W. (1957*a*). Insects in Southern Rhodesian tobacco culture. Part II. Insects occurring in the fields. Hymenoptera.—*Acta trop.* **14** pp. 236–243.

Bünzli, G. H. & Büttiker, W. W. (1957*b*). Insects in Southern Rhodesian tobacco culture. Part III. Insects occurring in the fields. Diptera.—*Acta trop.* **14** pp. 243–250.

Charles, V. K. (1941). A preliminary check list of the entomogenous fungi of North America.—*Insect Pest Surv. Bull. U.S.* **21** (suppl. to no. 9) pp. 707–785.

Dammerman, K. W. (1929). The agricultural zoology of the Malay Archipelago. —473 pp. Amsterdam, de Bussy.

DAVIS, J. J. (1919). Contributions to a knowledge of the natural enemies of *Phyllophaga*.—*Bull. Ill. nat. Hist. Surv.* **13** pp. 53–138.

DELACROIX, G. (1893). Observations sur quelques formes *Botrytis* parasites des insectes.—*Bull. Soc. mycol. Fr.* **9** pp. 177–184.

FITZPATRICK, H. M. (1930). The lower fungi. Phycomycetes.—331 pp. New York & London, McGraw-Hill.

FRIEDERICHS, K. (1913). Über den gegenwärtigen Stand der Bekämpfung des Nashornkäfers (*Oryctes rhinoceros* L.) in Samoa.—*Tropenpflanzer* **17** pp. 538–556, 603–619, 660–675.

GIARD, A. (1891*a*). L'*Isaria*, parasite de la larve du hanneton.—*C. R. Acad. Sci., Paris* **112** pp. 1270–1273.

GIARD, A. (1891*b*). Sur les cladosporiées entomophytes, nouveau groupe de champignons parasites des insectes.—*C. R. Acad. Sci., Paris* **112** pp. 1518–1521.

GIARD, A. (1893). L'*Isaria densa* (Link) Fries, champignon parasite du hanneton commun (*Melolontha vulgaris*, L.).—*Bull. sci. Fr. Belg.* **24** pp. 1–112.

HERGULA, B. (1930). On the application of *Metarrhizium anisopliae* against *Pyrausta nubilalis*.—*Sci. Rep. int. Corn Borer Invest.* **3** pp. 130–141.

MEÏER, N. F. (1940). The theoretical basis of the biological control method against injurious insects. [*In Russian.*]—*Bull. Pl. Prot., Leningr.* **1940** no. 1–2 pp. 143–152. (*Rev. appl. Ent.* (A) **30** p. 144.)

METSCHNIKOFF, E. (1879). Maladies des hannetons du blé (*Anisoplia austriaca*). [*In Russian.*] (Cited by Sweetman, 1936.)

MOUTIA, L. A. (1940). The search for parasites of white grubs (Melolonthids) in Zanzibar, Algeria, Morocco and France.—*Bull. ent. Res.* **31** pp. 193–208.

NORTHRUP, Z. (1914). A bacterial disease of June beetle larvae, *Lachnosterna* spp.—*Tech. Bull. Mich. agric. Exp. Sta.* no. 18, 37 pp.

PEMBERTON, C. E. (1939). Entomology.—*Rep. Comm. Exp. Sta. Hawaii. Sug. Pl. Ass. 1938–39* pp. 19–27. (*R.A.E.*, (A) **28** p. 460.)

PETCH, T. (1923). Studies in entomogenous fungi. III.—*Trans. Brit. mycol. Soc.* **9** pp. 108–128.

PETCH, T. (1924). Studies in entomogenous fungi. IV. Some Ceylon *Cordyceps*.—*Trans. Brit. mycol. Soc.* **10** pp. 28–44.

PETCH, T. (1937). Notes on entomogenous fungi.—*Trans. Brit. mycol. Soc.* **21** pp. 34–67.

PETCH, T. (1944). Notes on entomogenous fungi.—*Trans. Brit. mycol. Soc.* **27** pp. 81–93.

PETTIT, R. H. (1895). Studies in artificial cultures of entomogenous fungi.—*Bull. Cornell agric. Exp. Sta.* no. 97.

PICKLES, A. (1933). Entomological contributions to the study of the sugar-cane froghopper.—*Trop. Agriculture, Trin.* **10** pp. 222–233.

PRILLIEUX, E. & DELACROIX, G. (1891). Sur la muscardine du ver blanc.—*C. R. Acad. Sci., Paris* **113** pp. 158–160.

PYATNITZKIĬ, G. K. (1940). Agrotechnical methods of controlling the beet-weevil. [*In Russian.*] [*In*] KULAGIN, N. M. & PYATNITZKIĬ, G. K. *Ed.* The beet weevil and its control, pp. 25–37. (*R.A.E.*, (A) **30** p. 64.)

REX, E. G. (1940). A promising fungous pathogen of adult Japanese beetles (*Popillia japonica*).—*J.N.Y. ent. Soc.* **48** pp. 401–403. (*Rev. appl. Mycol.* **20** p. 462.)

ROCKWOOD, L. P. (1951). Entomogenous fungi of the genus *Metarrhizium* on wireworms in the Pacific northwest.—*Ann. ent. Soc. Amer.* **43** pp. 495–498.

RORER, J. B. (1910). The green muscardine of froghoppers.—*Proc. agric. Soc. Trin. Tob.* **10** pp. 467–482.

RORER, J. B. (1913). The green muscardine fungus and its use in cane fields.—*Circ. Bd Agric. Trin. Tob.* no. 8, 14 pp.

SCHAEFER, E. E. (1937). Locust fungi.—*Pamphl. S. Afr. biol. Soc.* no. 9, p. 21.

STEVENSON, J. A. (1916). Report of the Pathologist.—*4th Rep. Bd Comm. Agric. P. R. 1914–15* pp. 33–34.

SWEETMAN, H. L. (1936). The biological control of insects.—461 pp. Ithaca, N.Y., Comstock.

URICH, F. W. (1913). The sugar cane froghopper (*Tomaspis varia* Fabr.) and biological notes on some Cercopids of Trinidad.—*Circ. Bd Agric. Trin. Tob.* no. 9, 45 pp.

WALLENGREN, H. (1930). On the infection of *Pyrausta nubilalis* Hb. by *Metarrhizium anisopliae* (Metsch.) Sor. II.—*Sci. Rep. int. Corn Borer Invest.* **3** pp. 64–73.

© Commonwealth Agricultural Bureaux, 1959.

IMMATURE NUTFALL OF COCONUTS IN THE SOLOMON ISLANDS.

I.—DISTRIBUTION OF NUTFALL IN RELATION TO THAT OF *AMBLYPELTA* AND OF CERTAIN SPECIES OF ANTS.

By E. S. Brown

Commonwealth Institute of Entomology.

(Plates II & III.)

Contents.

	PAGE
Methods of survey	98
Ants and nutfall	100
The rôle of *Anoplolepis* and nutfall	101
Crop changes in palms of known history	101
Evidence from nutfall observation plots	102
Summary of evidence from the nutfall observation plots	109
Vidaka damage rates observed in selected areas	109
Data from miscellaneous plots and samples	111
An instance of nutfall associated with *Anoplolepis*	114
Evidence from the behaviour of *Anoplolepis* in presence of *Amblypelta*	114
Other species of ants and their relation to nutfall	116
The distribution of *Amblypelta* species and its relation to nutfall	119
Further considerations in assessing the extent of losses through *Amblypelta* attack	126
Loss of copra in surviving nuts	126
Losses due to plantations not being worked	127
Summary	128
Acknowledgements	128
References	129
Appendix A. Crop estimation	129
Appendix B. List of ants recorded from coconut plantations in the Solomon Islands	132

As a continuation of researches on coconuts in the British Solomon Islands Protectorate recently carried out by the late Dr. J. S. Phillips (1956), the author investigated the problem of immature nutfall of coconuts caused by the Coreid bug, *Amblypelta*. The greater part of these researches, carried out during the years 1954–56, was described in four Progress Reports, which were not published but were duplicated for limited circulation. Some of the subject matter of these reports, and in addition some results on certain aspects which have not been included in any reports hitherto, is of sufficient general entomological interest for wider circulation; in bringing all this material together for the present series of papers, certain passages from the reports have, in cases where further investigation has rendered no change necessary, been extracted *verbatim*, or only slightly modified or condensed.

The history of the study of immature nutfall * in the Solomon Islands has been reviewed by Phillips (*loc. cit.*) and no repetition is necessary here, except to stress the important biological rôle played by certain species of ants, which has figured conspicuously in that study. Briefly, there are, among the many species of ants that occur in coconut plantations in the islands, a limited number that tend to be dominant; these are to a large extent mutually exclusive, so that usually only one of them is dominant not only on any one palm, but often over large areas up to 100 acres or more. Since they forage all over the palms and come into contact with *Amblypelta* in the palm crowns, their action on this pest (antagonistic or otherwise) determines whether it can become established or not. Thus a given species of ant can be active and antagonistic in relation to *Amblypelta*, and thus protective as regards the coconut crop, or passive and non-protective. In the present paper, the term "protective" is used of any species of ant that is antagonistic to *Amblypelta* and that therefore protects the coconut crop from attack by the bug.

The importance of the study of the ants lies in the possibility it provides of trying indirectly to restrict the incidence of nutfall by first changing the ant population in such a way as to replace non-protective by protective species, and then leaving the latter to effect control of *Amblypelta*. At the outset of the author's studies there were good reasons for thinking that this line of approach was the most promising, and, if successful, likely to result in the most economical control.

The major distribution of nutfall by islands is primarily determined by that of the species of *Amblypelta*. Logically, therefore, this aspect should be treated first, but it will be necessary to deal with the distribution of nutfall in relation to that of ants, before certain aspects of its distribution by islands can be clearly understood.

Methods of Survey.

When examining a plantation, or any part of one, for the purpose of assessing losses caused by *Amblypelta*, it is necessary first to find out whether damage of this kind is occurring at all. This can be done by collecting a number of fallen nutlets from the ground (preferably not less than about 50), and seeing if any bear the characteristic scars caused by the feeding of *Amblypelta* (Pl. II, fig. 1); if more than 10 or 20 per cent. are scarred, one may expect some loss of crop to be associated. The intensity of nutfall, as measured by loss of crop, may vary from 0 to 100 per cent., and it is important to be able to make at least a rough assessment of this loss. This involves the difficulty of crop estimation. For the purposes of the work, it was necessary to be able to estimate crops quickly in the field, so as to cover moderately large areas within the often limited time available. The method adopted was a modification of one used by R. Leach (unpublished report to Messrs. Lever Bros., 1948), and is discussed in some detail in Appendix A (pp. 129–132). The figure arrived at from this method is the crop expressed as the number of nuts produced per palm per annum, which can be averaged for the whole or part of any area under consideration.

In order to assess the incidence of nutfall, however, it is insufficient merely to obtain an estimate of the crops of a given area, because cropping can be

* A proportion of the fruits formed by the coconut palm is always shed shortly after fertilisation, so that immature nutfall may to that extent be regarded as a natural process. For convenience, the term "nutfall" is employed in this paper, except where otherwise stated, in the sense in which it is used locally, to signify the condition characterised by a marked reduction in the number of nuts that reach maturity accompanied by the presence of the feeding scars of *Amblypelta* on those that are shed at an early stage of their development or that survive but remain undersized. Thus an area of coconut plantation in which this condition is prevalent is termed a nutfall area.

influenced by several factors other than *Amblypelta*, and notably by soil conditions. It is necessary to know what relation the existing crop bears to the potential crop in that area, that is, the crop as it would be in the absence of attack by *Amblypelta*. This is often impossible, and to obtain an accurate figure it would be necessary to compare crops from the same palms over more or less long periods (to average out seasonal variations) (a) when they were suffering from nutfall and (b) when they were not. This is scarcely practicable, since conditions for such observations seldom occur. However, it often happens that there is nutfall in one part of a plantation, but not in adjacent parts where a protective species of ant occurs, and in such cases, provided there are no obvious differences in soil or other conditions, it is reasonable to use the differences in crops as a basis for estimating losses due to nutfall. Although occasionally one might overlook an alternative factor modifying the crop, this is unlikely to be serious provided one generalises from observations from a sufficient number of localities.

A second method which has been used extensively in the present researches is what Vanderplank (1958) has called the " Vidaka Damage Rate ".* A quantity of fallen nutlets is collected from the ground below the palm and these are sorted into those with, and those without scars caused by the feeding of *Amblypelta*; the number bearing such scars, expressed as a percentage of the total, is the Vidaka Damage Rate (hereafter abbreviated as V.D.R.), which may vary from 0 to 100. Very broadly, the V.D.R. gives some indication of the intensity of *Amblypelta* attack, and therefore of the loss this causes. Discrepancies do occur, however; for instance, an area with a high V.D.R. may sometimes bear unexpectedly large crops. In some cases, this is due to the time factor, the crop at any one time reflecting, not the contemporary intensity of *Amblypelta* attack, but that which prevailed at a former period (up to nearly 12 months before) when the nuts now mature were at a vulnerable stage of growth. In other cases, however, any lack of correspondence between V.D.R. and contemporary crops must be due to other factors.

Two systems were used for recording data in the field:

(i) The first, used when surveying a plantation for the first time, was by means of " samples ". A sample was made by following a single line of palms through the plantation, and recording relevant data for every palm, or in the case of large plantations every third, fifth or tenth palm; by recording two or more such samples running across one another in selected directions it was possible to obtain a good idea of the condition of the plantation as a whole. The data recorded for each palm included the dominant species of ant, crop grade (see p. 130), V.D.R., evidence of *Amblypelta* scars on mature nuts (Pl. II, figs. 2, 3), vegetation (creepers, epiphytes), and other details not relevant to the subject matter of this paper. Provided these samples cover the plantation adequately, the data could be used to obtain an approximate idea of ant distribution, and to correlate with it the distribution of crops and intensity of *Amblypelta* attack.

(ii) The second system, used when it was required to record fuller details of limited areas, was by means of " plots ". A " plot ", in this sense, is a map showing the position of every palm in the area in question. Isometric graph paper, in which the points of intersection of the grid-lines are in the same relative positions as the palms in a plantation with " triangular " spacing (the normal

* *Kidaka* (plural, *vidaka*) is the Kiswahili word used in Zanzibar for the developing fruiting body of the coconut palm during the first three months after the opening of the spadix on which it is borne and thus includes both pre- and post-flowering stages, since fertilisation does not occur until 3–4½ weeks after the opening of the spadix (Vanderplank, 1958). Vanderplank, however, found no significant difference, as regards the proportion showing damage by *Pseudotheraptus wayi* Brown, the Coreid causing nutfall in Zanzibar, between vidaka in the pre-fertilisation stage and those in the post-fertilisation stage, in which natural shedding of the nutlets occurs.

condition in the European-type plantations in the Solomon Islands), was a convenient medium on which to record the positions of the palms; other relevant data could also be recorded by using suitable symbols and abbreviations. A " plot " has the advantage that at periodic subsequent checks the history of individual palms can be traced; this is very useful where the distribution of ants is undergoing change.

Ants and Nutfall.

Of the various species of ants that forage over coconut palms, four are more abundant than others and tend to dominate more or less large areas of plantation. These are *Oecophylla smaragdina* (F.), *Pheidole megacephala* (F.), *Iridomyrmex myrmecodiae* Emery and *Anoplolepis longipes* (Jerd.). Usually only one of these is dominant on any one palm, and even over large areas; two may sometimes occur together, but this is usually associated with instability in the population at the time. There are, of course, many other species of ants that turn up in plantations, and some of these will be discussed later.

With regard to *O. smaragdina*, *P. megacephala* and *I. myrmecodiae*, the current views on their relation to nutfall are accepted, namely, that *Oecophylla* protects palms effectively against *Amblypelta*, that the other two do not, and that one or other of the latter is therefore usually to be found where there is any nutfall. Certain reservations will later be made with regard to *Pheidole* and *Iridomyrmex* on San Cristobal (pp. 121–122). About *Anoplolepis*, however, there has always been some doubt. Although it appears to have been in the islands for at least 50 years, and was recorded " throughout the Solomons " by Mann (1919), there have been few observations concerning its relationship with nutfall. This fact itself suggests that *Anoplolepis* was nowhere very conspicuous during the ten years before the second world war, when a great deal of research was being carried out on *Amblypelta*. Phillips (unpublished) mentions that it spread rapidly at Karikana, on the island of Kolombangara, in 1936, and found evidence that it exercises some control over *Amblypelta*. It has, however, been known to natives for a long time, as indicated by the existence of names for it in most of their languages. An interesting story was told by an inhabitant of Hauhui, a village on the south coast of Malaita. He said that coconuts had been introduced to Malaita by his " grandfathers " (possibly about a hundred years ago) from Guadalcanal; at the same time the ant, *Anoplolepis*, which was not then known on Malaita, was introduced from Nggela, where it was known to be associated with good coconut crops. It is thus known to this day at Hauhui as *lolo Nggela*, " the ant from Nggela ". It is said to have survived at Ohne, a village about two miles from Hauhui, but not at Hauhui itself, in spite of several attempts at introduction. If this is true, then the status has remained the same to the present day, for a coconut grove at Ohne is occupied by *Anoplolepis*, while the dominant ant at Hauhui is *Iridomyrmex myrmecodiae*.

Anoplolepis has recently come into prominence. Phillips (1956) found that it had spread very considerably and rapidly in certain plantations on Guadalcanal; this spread must have taken place largely between 1948 and 1952, because O'Connor and Leach (O'Connor, 1950, p. 29) scarcely encountered it in these same plantations. Phillips was of the opinion that *Anoplolepis* gave some protection against *Amblypelta*, because in areas where it had replaced *Pheidole* there had been recovery from nutfall. However, he was not very confident, and was only able to conclude that it " destroyed *Amblypelta*, though not as effectively as did *Oecophylla* ".

There is by no means general agreement on the rôle played by *Anoplolepis*. It is of interest that, in Zanzibar, nutfall of a closely similar type is caused by *Pseudotheraptus wayi*, another Coreid bug that resembles *Amblypelta* in

appearance and habits. Although *Anoplolepis longipes* occurs there also, it has been found to give little or no protection against *Pseudothcraptus* (Way, 1951, 1953). The author's observations in the Solomon Islands, however, that there was no sign of nutfall over large areas dominated by *Anoplolepis*, coupled with Phillips' conclusions quoted above, suggested that the matter should be studied in more detail. Accordingly, experiments and observations were started with the object of demonstrating the rôle played by *Anoplolepis*, and also by certain species of ants that, while not dominant over large areas, were prominent locally.

The Rôle of *Anoplolepis longipes* and Nutfall.

The principal evidence concerning the rôle of *Anoplolepis* can be treated in a number of categories:

(a) Crop changes in palms of known history.
(b) Evidence from nutfall observation plots.
(c) Determinations of V.D.R. in selected areas.
(d) Data from miscellaneous plots and samples.
(e) Evidence from the behaviour of *Anoplolepis* in the presence of *Amblypelta*.

(a) Crop changes in palms of known history.

Some of the most direct evidence for the effect of various ant species on crop production, and therefore, by inference, on nutfall, is to be obtained from long-term observations of the crops produced by individual palms on which changes in the ant fauna have also been recorded. In nutfall areas, such records are only available for certain palms in the Kukum–Lunga–Tenaru area of Guadalcanal where nutfall has been principally studied in recent years. R. Leach (unpublished report to Messrs. Lever Bros., 1948) mapped a number of plots, indicating individual palms and the ants occupying them, and, in several of them, an estimate of the grade of the crops. These plots have now been re-examined. Of the palms in Leach's plots, 1,005 have been identified with certainty; of these, 339 were originally occupied by *Oecophylla smaragdina* and 666 by *Pheidole megacephala*; by 1954–55, *Oecophylla* had persisted in 87 palms, and been

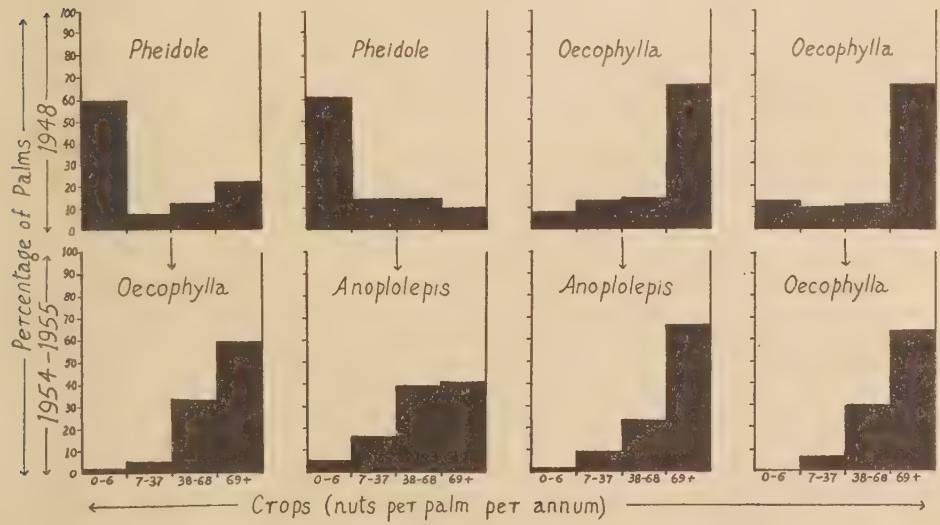


Fig. 1.—Changes in percentage of palms in different crop ranges, associated with different ant sequences.

replaced by *Anoplolepis* in 252, *Pheidole* had been replaced throughout, by *Oecophylla* in 135 palms, and by *Anoplolepis* in 531. There are thus four types of ant sequence: *Oecophylla* → *Oecophylla*, *Oecophylla* → *Anoplolepis*, *Pheidole* → *Oecophylla*, and *Pheidole* → *Anoplolepis*. Since *Oecophylla* is known to be a protective ant, associated with good crops, and *Pheidole* a non-protective one, associated with nutfall, comparison of crop changes associated with these ant sequences should throw light on the rôle played by *Anoplolepis* as regards nutfall.

The changes in crop associated with different ant sequences are compared diagrammatically in fig. 1, where the percentage of the palms falling into each of four different ranges of crops is shown in histogram form for each ant sequence separately. It can be seen from this that there has been considerable improvement in crops when *Pheidole* has been replaced by either *Oecophylla* or *Anoplolepis*. On the other hand when *Oecophylla* has either remained in occupation or been replaced by *Anoplolepis*, the crops have remained substantially the same.

In the case of palms originally occupied by *Oecophylla*, there was actually an improvement in crop averages, no matter whether the *Oecophylla* was replaced by *Anoplolepis* or not; this was probably due to *Oecophylla*'s having only recently replaced *Pheidole* in some of the palms in 1948, so that their crops had not then recovered fully from the nutfall associated with the latter ant.

Of the palms occupied originally by *Pheidole*, the final condition of crops was better in those which *Oecophylla* had come to occupy than in those with *Anoplolepis*; however, a study of the histograms shows that these palms also started off with better crops. Taking the crop average in nuts per palm per annum for all palms together, the following figures were obtained:

Ant change	Crop average, 1948	Crop average, 1954–55
Pheidole→*Oecophylla*	30	75
Pheidole→*Anoplolepis*	22	55

It can be seen that in each case the crop average increased to 2½ times its initial value. The lower crops in the *Anoplolepis* palms during both periods are very probably due to their being situated on poorer soils.

It is a little unfortunate that these data all come from a recovery area, where nutfall has been decreasing, and that no evidence is available at present from the converse change, where areas bearing good crops have changed to nutfall ones. However, it is safe to summarise available evidence by stating that *Anoplolepis* is protective against *Amblypelta*, and certainly approaches *Oecophylla* in this respect, although we cannot compare them closely enough to state that it gives equal protection.

(*b*) *Evidence from nutfall observation plots.*

In the plantations at Kukum and Tenaru, on Guadalcanal, there are large areas occupied by *Anoplolepis* and others by *Oecophylla*, and amongst them are certain smaller, yet considerable, areas occupied by *Iridomyrmex myrmecodiae* and affected by nutfall. Opportunity thus occurred to compare the effect upon nutfall of *Anoplolepis* with that of *O. smaragdina*, a protective species, on the one hand, and with that of *I. myrmecodiae*, a non-protective species, on the other. With this object, ten nutfall observation plots, five at Tenaru and five at Kukum, were selected at the end of 1954, and continuous observations were maintained on them for about a year. Each plot consisted of seven palms, which were numbered, and a wire fence was erected on an outer ring of palms (Pl. II, fig. 4).

At regular intervals, all fallen nutlets and mature nuts were collected from

the ground, sorted into those with and those without *Amblypelta* scars, counted and recorded, not only for each plot, but for each palm individually. To begin with, collections were made approximately once a week, care being taken to arrange a collection on the last day of each month to obtain monthly totals. The objects were to obtain records, over a period, of the extent of attack by *Amblypelta* (as indicated by the V.D.R.) and of the crops produced (as indicated by the number of nuts matured). After a time it became evident that some of the mature nuts were being lost through theft, and that the data for crops were therefore unreliable. Accordingly, from then on the mature nuts were harvested from the palms by climbers; this was started in May 1955 for the Tenaru plots, and in July 1955 for the Kukum plots, and harvesting was carried out after those dates at approximately two-monthly intervals, the number of spadices removed and the number of nuts per spadix being recorded for each palm separately. The nutlets were latterly collected twice a month, once in the middle and once at the end.

The selection of sites for the plots was such as to compare the effects of the different ants under as nearly as possible equivalent conditions. They were given reference letters and numbers as follows:—

	Tenaru	Kukum
Anoplolepis	A.1, A.2	A.3, A.4
Oecophylla	O.1	O.2
Iridomyrmex	X.1, X.2	X.3
Iridomyrmex and *Oecophylla*, mixed ...		M.1

The Tenaru plots were ranged round the margin of the large nutfall (*Iridomyrmex*) area there (see Phillips, 1956, fig. 1), and were in two groups:

(1) A.1 and X.1 were near the western end, about 100 yards from each other, X.1 just inside and A.1 just outside the *Iridomyrmex* border. X.1 was selected deliberately in an area where *Anoplolepis* was encroaching upon *Iridomyrmex* territory, and, as was expected, was later overrun by *Anoplolepis* during the course of the observations. It was therefore possible to trace the change in nutfall and correlate it with the change in ants.

(2) A.2, O.1 and X.2 were all near the eastern border of the *Iridomyrmex* area. X.2 was 40 yards inside the border; A.2 was 50 yards outside the border and 100 yards from X.2, while O.1 was 150 yards outside the border and the same distance from A.2. A.2 was therefore closer to the nutfall area than O.1 and probably in greater danger of attack by *Amblypelta*.

The Kukum plots were in three groups:

(1) A.3 and X.3 were on either side of the southern border of an *Iridomyrmex* area of just over 20 acres; X.3 was about 70 yards inside and A.3 40 yards outside the border, and they were about 240 yards from each other. On some of the palms in A.3, *Anoplolepis* was later replaced by other ants.

(2) M.1 was on the northern border of the *Iridomyrmex* area. At the beginning of the observations 4 palms were occupied by *Oecophylla* and 3 by *Iridomyrmex*, but the latter ant later invaded the *Oecophylla* palms.

(3) A.4 and O.2 were 30 yards apart and both about 150 yards from the nearest margin of the *Iridomyrmex* area. After the beginning of observations, *Oecophylla* took possession of certain palms in A.4.

For purposes of analysing the results obtained during 1955, all these plots are best considered in groups as follows:—

Plots A.1, A.2, O.1 and X.2 (Tenaru).—These plots were all situated under comparable conditions at Tenaru, the last three being close together and about half a mile distant from the first; all were on apparently similar soil, and close to the border-line between nutfall and non-nutfall areas, so that there is no

doubt that *Amblypelta* had good chances of access to all of them. The only difference was in the species of ant occupying the palms.

The details of the fallen nutlets and mature nuts collected are shown in Table I. Turning first to the records of nutlets collected, we find that in the

TABLE I.

Fallen nutlets collected, and mature nuts harvested, from plots with *Anoplolepis* (A.1, A.2), *Oecophylla* (O.1) and *Iridomyrmex* (X.2) at Tenaru, showing the number and percentage with *Amblypelta* scars.

	Anoplolepis plots				*Oecophylla* plot		*Iridomyrmex* plot	
	A.1		A.2		O.1		X.2	
	s	*u*	*s*	*u*	*s*	*u*	*s*	*u*
Fallen nutlets (total collected Jan.–Dec. 1955)								
Scarred (*s*) and unscarred (*u*) ..	1	494	12	457	0	304	807	188
Total	495		469		304		995	
% with *Amblypelta* scars	0·20		2·62		0		81·10	
Mature nuts (total harvested May 1955–April 1956)								
Scarred (*s*) and unscarred (*u*) ..	3	918	2	935	0	708	237	88
Total	921		937		708		325	
% with *Amblypelta* scars	0·33		0·21		0		72·92	

Iridomyrmex plot (X.2) the percentage with *Amblypelta* scars was very high (81·10) while in the *Oecophylla* plot it was nil and in both *Anoplolepis* plots it was very low (0·20 and 2·62). In plot A.2, nearly all the scarred nutlets were obtained from two adjacent palms on the same date, suggesting a chance invasion by one or two individuals of *Amblypelta* that managed to feed for a limited period before being discouraged by *Anoplolepis*. As A.2 was closer to the *Iridomyrmex* border than was O.1, this is not surprising. The larger total number of fallen nutlets in the *Anoplolepis* plots as compared with O.1 is not easy to explain, but it is clearly not due to *Amblypelta*. In any case it does not appear to affect the crops adversely, as indicated by the numbers of mature nuts (Table I); these were harvested over a period of approximately one year, beginning a few months after the start of the similar period during which the fallen nutlets were collected, so that these mature nuts had largely been in the young, susceptible stages when the nutlets were collected. The crops of mature nuts in both *Anoplolepis* plots were actually greater than those in the *Oecophylla* plot, which may have been due to a tendency of the latter to become waterlogged in wet weather.

Plots A.4, O.2 and X.3 (Kukum).—The same remarks apply to this series of plots at Kukum as to the first series at Tenaru, except that the *Iridomyrmex* plot is further removed from the others. The *Anoplolepis* and *Oecophylla* plots, however, are in this case closely adjacent, separated only by the width of a track, and conditions may be assumed to be as nearly identical as one could find. About September 1955, *Oecophylla* supplanted *Anoplolepis* in the crowns of three of

the palms in plot A.4, but this partial change for a limited part of the period of observation can have had but little effect on the figures obtained.

Records of fallen nutlets and mature nuts collected are given in Table II; it will be seen that, as before, there is a very high percentage of scarred material

TABLE II.

Fallen nutlets collected, and mature nuts harvested, from plots with *Anoplolepis* (A.4). *Oecophylla* (O.2) and *Iridomyrmex* (X.2) at Kukum, showing the number and percentage with *Amblypelta* scars.

	Anoplolepis plot		*Oecophylla* plot		*Iridomyrmex* plot	
	A.4		O.2		X.3	
	s	*u*	*s*	*u*	*s*	*u*
Fallen nutlets (total collected Jan.–Dec. 1955)						
Scarred (*s*) and unscarred (*u*)	0	309	0	190	1754	336
Total	309		190		2090	
% with *Amblypelta* scars	0		0		83·91	
Mature nuts (total harvested July 1955–June 1956) ..						
Scarred (*s*) and unscarred (*u*)	7	1170	0	1181	314	58
Total	1177		1181		372	
% with *Amblypelta* scars	0·59		0		84·4	

from the *Iridomyrmex* plot, while not a single scarred nutlet was recorded from either the *Anoplolepis* or the *Oecophylla* plots. Again, the total number of fallen nutlets is greater in the *Anoplolepis* than in the *Oecophylla* plot, but it does not appear to have had any effect on the crops of mature nuts, which are practically identical in the two plots. The occurrence of a few scars on mature nuts in A.4 shows that *Amblypelta* has in fact had access to this area, but *Anoplolepis* has effectively prevented it from becoming established and doing any serious damage.

Plot X.1 (Tenaru).—This plot is of peculiar interest since it was right on the border-line between *Anoplolepis* and *Iridomyrmex* areas, at a point where the former was advancing into *Iridomyrmex* territory; and although at the start of observations (December 1954) all palms were inhabited by *Iridomyrmex*, by the end of 1955 *Anoplolepis* had completely replaced it; the latter ant first took possession of the trunk bases and gradually extended upwards and invaded the crowns.

In Table III the changes in ants, fallen nutlets and mature crops have been traced through this transition period. It will be seen that with the replacement of *Iridomyrmex* by *Anoplolepis* there is a decrease in total fallen nutlets, and in the percentage of them bearing *Amblypelta* scars. The latter actually decreased to a steady 0 per cent. before *Iridomyrmex* had been driven out of the crowns of all the palms and for the whole year 1955 was only 1·63 per cent.; this is possibly explained by the fact that palms adjacent to others inhabited by a protective ant species may themselves derive some degree of collective protection, even although they are tenanted by non-protective species; this is not always true, however, as

TABLE III.

Records of fallen nutlets, crops and percentages of mature nuts with *Amblypelta* scars from plot X.1 over the period when *Iridomyrmex* was being replaced by *Anoplolepis*.

		xii.1954	i.1955	ii.1955	iii.1955	iv.1955	v.1955	vii.1955	x.1955	xii.1955
Ants on trunk	No. of palms with *Anoplolepis* ..	0	3	4	6	6	7	7	7	7
	No. of palms with *Iridomyrmex* ..	7	4	3	1	1	0	0	0	0
Ants in crown	No. of palms with *Anoplolepis* ..	0	No records				4	4	7	7
	No. of palms with *Iridomyrmex* ..	7					3	3	1 (mixed)	0
Fallen nutlets	Total	62	59	61	51	23	35	20	21	17
	% scarred	27·4	8·5	0	2·0	0	0	0	0	0
Mature nuts	Total	29	38	19	27	21	108*	145*	101*	79*
	% scarred	20·7	26·3	36·8	11·1	33·3	7·4	0·7	6·9	2·5

* From May 1955 onwards, mature nuts were harvested direct from the palm crowns, and the figures represent the crops reaching maturity during the periods intervening between harvesting dates.

shown in the discussion of Plot M.1, below. The figures for crops of mature nuts do not provide a clear picture, since in the first part of the period the nuts were collected after falling to the ground, whereas in the later part they were harvested from the palms, and consistent increases in crops can hardly be expected within the period covered; but it is significant that there has been a very substantial decrease in the proportion of mature nuts that are scarred; as is to be expected, this decrease occurred somewhat later than the corresponding decrease in the proportion scarred amongst the fallen nutlets, since many of the nuts that matured and were harvested later had acquired scars when in the young stage, at a time when *Iridomyrmex* had been the only ant present.

The part of the *Iridomyrmex* area in which this plot is situated did not, in fact, suffer heavily from nutfall even at the start of the observations. It is interesting to note, however, that in December 1955, by which time the V.D.R. inside the plot had been reduced to zero, a collection of fallen nutlets from the adjacent area still occupied by *Iridomyrmex* showed a V.D.R. of 23·7, which is very close to the figure (27·4) obtained inside the plot at the start of observations twelve months before.

We may summarise the evidence from this plot by concluding that immediate protection against *Amblypelta* can be given by *Anoplolepis* once it becomes firmly established; observations were not continued long enough to show any permanent improvement in crop production.

Plot A.3 (*Kukum*).—This plot proved a rather unsatisfactory one from some points of view. In January 1955, the trunks of all palms were occupied by *Anoplolepis* and the plot was selected because it was very close to an *Iridomyrmex* area with heavy nutfall (including plot X.3). After a month or two, a fair proportion of the fallen nutlets were found to bear *Amblypelta* scars, and a closer examination, especially of the crowns of the palms, showed that the *Anoplolepis* colonies were weak and not well established and that other species of ants were present. Thereafter the species of ants in the crowns were checked at intervals, and at different times no less than six were recorded apart from *Anoplolepis*, namely, *Oecophylla smaragdina*, *Camponotus irritans* (F. Sm.) var. *samoaensis* Santschi, *C. reticulatus* Roger var. *bedoti* Emery, *Bothriomyrmex pusillus* (Mayr), *Monomorium floricola* (Jerd.), and an unidentified ant (? *Pheidolacanthinus* sp.). On May 14th, and again on September 23rd, only three of the seven palms had *Anoplolepis* in the crown. Some of these species are known to be non-protective and therefore, in spite of occasional occurrence of small numbers of *Oecophylla* in some of the crowns, it is not surprising that nutfall was appreciable. Out of a total of 627 fallen nutlets collected from January to December 1955, 164 were scarred, giving a V.D.R. of 26·16. In 1956 the V.D.R. rose higher; out of 694 nutlets collected from January to October, 359 were scarred, giving a V.D.R. of 51·73.

Experience elsewhere has shown that the species of ants listed above are among those typical of transition zones between areas occupied by different principal species, and if one of these areas is affected by *Amblypelta* the transition zone usually suffers from moderate nutfall.* Protective species may be present, but not in sufficient numbers to give complete protection. On only one occasion was *Amblypelta* actually observed by climbers in plot A.3, and it is of interest that only adults were present. There was no sign of nymphs, and it is possible that the nutfall was caused by periodic immigrations of adults from the heavily infested *Iridomyrmex* area adjacent; they could doubtless manage to feed for a limited period on young nuts, but would probably soon be discouraged sufficiently to prevent their breeding.

* The term "moderate nutfall" is used in this series of papers to denote the loss of an appreciable part of the potential crop over a given area, within which individual palms may be affected to varying degrees, some possibly severely.

In spite of the moderate nutfall occurring in this plot, it is interesting to note that crops of mature nuts remained high; from July 1955 to June 1956, a total of 1,049 nuts was harvested, which is not very much less than the figures obtained for plots A.4 and O.2, which were completely or almost completely protected (Table II); 201, or 19·16 per cent., were scarred. The total numbers harvested were decreasing, however, at the end of the period in question; this fact, and the increase in V.D.R. in 1956 as compared with 1955, indicate that the plot had been better protected up to the period when observations began.

The points of greatest interest learned from this plot are that *Anoplolepis* does not give good protection against *Amblypelta* attack unless it is well established on all, or nearly all, the palms; and that a V.D.R. of as much as 25 and perhaps more does not necessarily reflect a severe reduction of crops.

Plot M.1 (Kukum).—This plot at Kukum differs from the others in that its ant population was mixed from the start, three palms being occupied by *Iridomyrmex* and suffering from heavy nutfall, and four being occupied by *Oecophylla* and bearing reasonably good crops. The main object, apart from comparing the relation of the two ants to nutfall under conditions as nearly identical as possible, was to find out, on the one hand, whether the protective effect of *Oecophylla* will extend to adjacent unprotected palms, and on the other, to ascertain to what extent *Amblypelta* can cross the *Oecophylla* border and produce nutfall in a palm that should be protected by the latter species.

Records from this plot were started at the beginning of 1955 and continued until July 1956. It was found before the end of 1955 that *Iridomyrmex* had started to invade the *Oecophylla* palms; it was on the trunks of some, and in December it appeared in the crown of one; in June 1956, it was present in the crown of every palm in the plot, and its effect, as reflected by the degree of nutfall and by crop size, had become obvious. For the present analysis, therefore, only the counts made up to September 1955, for fallen nutlets, and up to December 1955, for mature nuts, were included.

The data from the fallen nutlets (Table IV) show that the protective effect of *Oecophylla* on adjacent *Iridomyrmex* palms is at most very slight, for the

TABLE IV.

Fallen nutlets collected and mature nuts harvested from mixed plot M.1 at Kukum, showing the number and percentage with *Amblypelta* scars.

	Palms 1–3 (*Iridomyrmex*)		Palms 4–7 (*Oecophylla*)	
Fallen nutlets (total collected Feb.–Sept. 1955)	*s*	*u*	*s*	*u*
Scarred (*s*) and unscarred (*u*) ..	900	125	10	97
Total	1025		107	
% with *Amblypelta* scars ..	87·80		9·35	
Mature nuts (total harvested July–Dec. 1955)				
Scarred (*s*) and unscarred (*u*) ..	35	1	15	364
Total	36		379	
% with *Amblypelta* scars ..	97·22		3·96	

percentage of scarred nutlets from palms 1–3 is very high (87·8); on the other hand, the ability of *Amblypelta* to produce nutfall on the *Oecophylla* palms is also very slight, although it is interesting that a few scarred nutlets occur; the same thing is found in the mature nuts. Thus *Amblypelta* can occasionally survive long enough to produce a few scars even on a palm strongly held by *Oecophylla*.

Summary of evidence from the nutfall observation plots.—As far as the main object of these plots is concerned, namely the comparison of *Anoplolepis* with other ants as regards its relation to nutfall, the data provide clear evidence that *Anoplolepis* gives a high degree of protection against *Amblypelta*. In fact, they suggest strongly that the degree of protection given by this ant, provided it is well established and present in strength, is nearly if not quite equal to that given by *Oecophylla*; furthermore that, other things being equal, palms occupied by *Anoplolepis* can produce as good crops as those occupied by *Oecophylla*. On this last point, however, it would be unwise to draw conclusions too confidently, owing to the possibility of there being undetected differences between the plots in the nature of the soil and the hereditary constitution of the palms.

A minor point of interest brought to light is that neither *Anoplolepis* nor *Oecophylla* gives 100 per cent. protection against *Amblypelta*, particularly if the latter is abundant in closely adjacent areas or the ants are not established in strength. This is especially true of transition zones between principal ant species, where a mixture of several usually unimportant species may occur.

(*c*) *Vidaka damage rates observed in selected areas.*

In addition to the counts of fallen nutlets in the nutfall observation plots, occasional collections have also been made in other places, specially selected for comparison of areas occupied by *Anoplolepis* with those occupied by other ants. The actual numbers collected are of no significance, because the areas were not all of the same size, and no attempt was made to collect every nutlet, but merely a sufficient number for estimating the V.D.R.

The areas chosen were in three different plantations, Rua Vatu and Tenaru on Guadalcanal, and Baunani on Malaita. In each plantation a number of areas was selected, including some with the palms occupied by *Anoplolepis* and others occupied by other ants (protective and non-protective); for purposes of comparison, areas with the different ant species were selected closely adjacent to one another, so that they were presumably equally accessible to *Amblypelta*. All figures obtained are given in Table V.

Rua Vatu.—Collections were made from 11 areas in all (Table V, areas 1–11), four dominated by *Anoplolepis*, one by *Oecophylla*, three by *Pheidole megacephala*, two by *Iridomyrmex*, while one was in a transition zone with a mixed ant population.

Comparing the V.D.R. for the different ant species, we find that in the *Anoplolepis* areas it varies from 1·3–8·6, in the *Pheidole* areas from 41·5–93·8, in the *Iridomyrmex* areas from 68·0–87·8 and in the single mixed area it is 50·0. It is unfortunate that only one very small area could be found which had a pure *Oecophylla* population and was adjacent to nutfall areas, so that the figures for this ant, although indicating 0 per cent. scarred nutlets, cannot be taken as strongly significant. Although *Oecophylla* is common in this plantation, it mostly occurs in areas of mixed ant populations; it is interesting to note that collections from beneath individual palms occupied by *Oecophylla* in such mixed areas usually yield a small percentage of scarred nutlets, comparable with that found in the *Anoplolepis* areas.

In some of the *Anoplolepis* areas this ant is not present in great strength, so

that it is not surprising that these areas are slightly vulnerable to *Amblypelta* attack. The relatively small amount of scarring, however, is not likely to increase total nutfall by much, and the effect of *Amblypelta* on crop production in these areas must be negligible, although there was a strong population of the bug in the plantation as a whole. It is of interest to note that area 2 was closely adjacent

TABLE V.

Comparison of percentages of fallen nutlets bearing *Amblypelta* scars in areas occupied by different ants.

No. of area		Ant present	No. of fallen nutlets collected	Nutlets with *Amblypelta* scars		Av. no. of scars per 100 nutlets
				No.	%	
Rua Vatu	1	*Anoplolepis longipes*	78	1	1·3	1·3
	2	„ „	209	18	8·6	44·9
	3	„ „	255	9	3·5	9·3
	4	„ „	88	4	4·5	7·9
	5	*Oecophylla smaragdina*	10	0	0·0	0·0
	6	*Pheidole megacephala*	204	97	47·5	144·1
	7	„ „	274	257	93·8	no record
	8	„ „	212	88	41·5	152·8
	9	Mixed, including *Pheidole*, *Technomyrmex* and *Oecophylla*	210	105	50·0	191·4
	10	*Iridomyrmex myrmecodiae*	231	157	68·0	245·5
	11	„ „	278	244	87·8	340·0
Tenaru	12	*Anoplolepis longipes*	47	0	0·0	0·0
	13	„ „	109	5	4·6	15·6
	14	*Oecophylla smaragdina*	100	0	0·0	0·0
	15	*Iridomyrmex myrmecodiae*	76	18	23·7	105·3
	16	„ „	48	42	87·5	360·4
Baunani	17	*Anoplolepis longipes*	57	0	0·0	0·0
	18	*Iridomyrmex myrmecodiae*	213	190	89·2	no record

to one in which *Iridomyrmex* was found to have persisted in the crowns of some of the palms in which *Anoplolepis* had invaded the trunk; it is not impossible that the same thing may have occurred occasionally in area 2, which would explain the somewhat higher percentage of scarring than is usual in *Anoplolepis* areas.

The total number of scars on each scarred nutlet was also recorded in these counts, and from these figures the total number of scars per 100 nutlets was calculated. In the *Anoplolepis* areas, apart from area 2, this figure did not exceed 10, while in all the *Pheidole* and *Iridomyrmex* areas it was well over 100, rising as high as 340 in one of the latter. This statistic may give a better measure of the intensity of *Amblypelta* attack, and it is suggested that a value of about 50 may be the threshold, above which *Amblypelta* attack begins to have an appreciable influence on crop production. This is a purely arbitrary figure, however, and the true value may well be higher.

Tenaru.—Collections were made (Table V, areas 12–16) from two *Anoplolepis* areas, one *Oecophylla* and two *Iridomyrmex*. All the areas were either within the large *Iridomyrmex* area (no. 15 near the west, and 16 near the east, end) or just outside it (no. 12 close to no. 15, and nos. 13 and 14 close to no. 16 and to each other). Values of the V.D.R. are 0 and 4·6 for the two *Anoplolepis*

areas, 23·7 and 87·5 for the *Iridomyrmex*, and 0 for the *Occophylla*. For some unexplained reason, nutfall is less severe in the western part of the *Iridomyrmex* area, and the value 23·7 is low for an area inhabited by this ant; in the eastern part, nutfall is more severe, and the value 87·5 is high. The low value of 4·6 for the closely adjacent *Anoplolepis* area is noteworthy. It will be noted that the total scars per 100 nutlets is over 100 for both *Iridomyrmex* areas, while the maximum figure for *Anoplolepis* is 15·6.

Baunani.—Collections were made (Table V, areas 17 and 18) from only one *Anoplolepis* and one *Iridomyrmex* area, very close together with a sharp borderline between them. The contrast in the V.D.R. (zero for *Anoplolepis* and 89·2 for *Iridomyrmex*) is of great significance. Counts of the total numbers of scars were not made here.

On the whole, the evidence from these observations of the V.D.R. in selected areas is in accordance with that from other sources considered so far, namely, that *Anoplolepis* gives adequate protection against *Amblypelta* provided it is present in strength.

(*d*) *Data from miscellaneous plots and samples.*

Apart from the investigations that were especially designed to throw light on the relation of *Anoplolepis* to nutfall, a considerable amount of more circumstantial evidence on this point has accumulated from general surveys made in widely separated parts of the Protectorate.

For the purposes of this discussion, a selection has been made of those plots and samples that permit comparison between the four principal ant species in their relation to crops and nutfall, with particular reference to *Anoplolepis*. They may be treated in two series, those in which nutfall attributable to *Amblypelta* is involved (mainly areas with a mixed ant fauna and moderate nutfall), and those in areas in which *Amblypelta*-induced nutfall does not occur. The first series enables *Anoplolepis* to be compared with other ants, as regards the average crops on palms inhabited by each species, and the V.D.R. The second series is selected with the object of comparing crops associated with *Anoplolepis* and with other ants, under conditions where *Amblypelta* is not a factor controlling yield. Figures obtained are given in Table VI.

TABLE VI.

Comparison of crops and V.D.R. in areas with and without nutfall, on palms occupied by ant species as shown.

	Details recorded	*Anoplolepis longipes*	*Oecophylla smaragdina*	*Iridomyrmex myrmecodiae*	*Pheidole megacephala*
22 plots and samples with moderate nutfall	Total no. of palms	1327	898	691	902
	Average crops (nuts per palm per annum)	37	55	22	24
	Total fallen nutlets	1152	868	918	1842
	V.D.R.	7·5	12·2	79·8	80·2
22 plots and samples without nutfall	Total no. of palms	2133	1208	61	54
	Average crops (nuts per palm per annum)	61	64	57	69

Plots and samples with moderate nutfall.—In the series exhibiting *Amblypelta*-induced nutfall, all plots and samples in which *Anoplolepis* was present have been included. Some of these have *Iridomyrmex* and some *Pheidole* as the main non-protective ant, and some have a mixture of the two.

It will be seen from the totals that although the V.D.R. is actually lower for *Anoplolepis* than for *Oecophylla* palms (7·5 as compared with 12·2), the crops on these palms are also considerably lower (averaging 37 nuts per palm per annum as compared with 55). It appears from this that there may be factors operating against crop production in palms occupied by *Anoplolepis* as compared with those occupied by *Oecophylla*, but that *Amblypelta* is not one of these factors, because in areas of moderate nutfall the extent of its attack is at least as great in *Oecophylla* as in *Anoplolepis* palms. Possible reasons for the difference in crops will be discussed below.

Crop estimates for *Pheidole* and *Iridomyrmex* palms are much lower (24 and 22 nuts, respectively, per palm per annum), and the V.D.R. is much higher (80·2 and 79·8); the crop estimates for palms carrying these two ants may in fact seem rather high seeing that they give little or no protection, but it must be remembered that these are areas of only moderate nutfall with mixed ant populations, and a certain degree of collective protection may be derived from the proximity of palms occupied by *Oecophylla* and *Anoplolepis*. For areas of severe nutfall, with a homogeneous population of *Pheidole* or *Iridomyrmex* over a wide area, crops are usually very much lower.

Plots and samples without Amblypelta*-induced nutfall.*—We are concerned here only with the crops associated with different ant species, and since the main question at issue is the comparison of crops associated with *Anoplolepis* with those associated with *Oecophylla*, only plots and samples in which these two ants are both more or less well represented have been selected for analysis.

As is to be expected in areas of palms not attacked by *Amblypelta*, crops associated with all species of ants tend to be higher and more nearly equal. The similarity between estimates associated with the four principal ants (*Anoplolepis*, *Oecophylla*, *Pheidole* and *Iridomyrmex*) is particularly striking (61, 64, 69 and 57 nuts, respectively, per palm per annum). The figures for *Pheidole* and *Iridomyrmex* are naturally based on few palms because it is usually only when they occur in a very limited number of palms that the latter do not exhibit nutfall. The figures for *Anoplolepis*, however, are based on large numbers of palms (2,133), often extending over large areas, which, being dominated by this ant, do not suffer from *Amblypelta* attack. The small difference of three nuts per palm per annum between *Anoplolepis* and *Oecophylla* palms is not likely to be significant.

One fact emerging from these data which seems to call for explanation is the low value for crop estimates associated with *Anoplolepis*, as compared with *Oecophylla*, in the areas of moderate nutfall. There are a number of considerations which might well contribute towards an explanation, although there is no concrete proof to support any of them:—

(1) In several of the nutfall areas, *Anoplolepis* is in process of invading areas occupied by *Pheidole* and *Iridomyrmex*. Many of the palms that were occupied by *Anoplolepis* when the crops were estimated had doubtless until quite recently been occupied by one of these non-protective ants, and there had been insufficient time for increase in crops to become evident; it takes several months for nuts to develop from the small stages, vulnerable to *Amblypelta*, to the mature condition on which crop estimates are based.

(2) It is possible also that in some cases, although *Anoplolepis* was present on the trunk, the crown was still occupied by *Iridomyrmex*, which was not detected during the survey. Evidence has been obtained that *Iridomyrmex* can

remain in possession of the crown, although cut off from the ground by *Anoplolepis* colonies at the base of the trunk, for periods up to 18 months.

(3) In some of the transition areas, *Anoplolepis* colonies may not yet have built up to sufficient numbers to give maximum protection against *Amblypelta*.

(4) There is some indication that *Anoplolepis* tends to be associated with soil conditions unfavourable to the coconut palm. Being a ground-nesting ant, dry soil conditions are most favourable to it, while in wetter soils usually associated with better crops the tree-nesting ant, *Oecophylla*, tends to remain dominant.

A large linear plot in Maraunia plantation on Guadalcanal provides a good illustration of this. An area of *Iridomyrmex* at one end with severe nutfall and very poor crops, and one of *Oecophylla* at the other end with good crops and no nutfall, were separated by an area, occupied by *Anoplolepis*, which had mediocre crops but was quite free from nutfall; the mediocre crops were clearly due to dry soil conditions, many of the palms being stunted and tapered. The data recorded for the three areas were as follows:—

	Iridomyrmex	*Anoplolepis*	*Oecophylla*
Crops (nuts/palm/annum)	6	29	55
V.D.R.	119/127 = 94	0/333 = 0	0/77 = 0

It is probably, in many cases, this correlation between *Anoplolepis* and poor soils that has given rise to a common belief that *Anoplolepis* is responsible for poor crops, but the effect is not one of direct cause and effect.

(5) Although *Anoplolepis* may give as good protection as *Oecophylla* against *Amblypelta*, there may be other pests against which it provides less protection. There is some indication that this is true of *Brontispa*, but this possibility needs further study.

The first three of the above considerations would apply in the areas of moderate nutfall, but not in areas where *Amblypelta*-induced nutfall does not occur, and they might therefore well afford the explanation demanded by the differences in the crop values from these two sources.

Certain data are of particular interest in connection with the relation between *Anoplolepis* and nutfall. One sample at Hulo (Malaita) is especially striking; it consisted of a single line of 167 palms running from one end of the plantation to the other through apparently very homogeneous soil conditions. *Anoplolepis* (A) and *Iridomyrmex* (I) alternate, with several changes along the line, the sequence, which included two palms occupied by *Oecophylla* (O), being as follows:—

A, 3; I, 1; A, 2; I, 41; A, 1; I, 1; A, 33; I, 3; A, 3; I, 38; A, 10; O, 1; A, 5; I, 1; O, 1; I, 23.

The general health of the palms was similar throughout, and yet the difference in crops on *Anoplolepis* palms (87 nuts/palm/annum) and *Iridomyrmex* palms (16 nuts/palm/annum) was very striking; the change in crops along the line as one ant gave place to the other was very sharp, and left no room for doubt about the protective effect of *Anoplolepis*. In an adjacent plot without nutfall, occupied only by *Anoplolepis* and *Oecophylla*, the average crops on palms occupied by the former were as high as 73 nuts/palm/annum, although there must have been plenty of *Amblypelta* in the area.

Another plot on Malaita was occupied by an intricate mixture of ants in which *Anoplolepis*, *Oecophylla* and *Iridomyrmex* were all well represented (87, 107 and 78 palms, respectively); there was scarcely any change in distribution between September 1954 and May 1955, so that on the latter date the ant population had been stable for some time. The *Iridomyrmex* palms showed heavy nutfall (V.D.R. 86·2), indicating a strong *Amblypelta* population; in spite

of this, the V.D.R. for the *Anoplolepis* palms was only about the same as that for *Oecophylla* palms (10·9 and 9·3, respectively).

In an area of Mamara plantation (Guadalcanal), large numbers of palms were occupied by *Anoplolepis*, *Occophylla and Iridomyrmex* (126, 192 and 159 palms, respectively), but these ants were distributed in better-defined, discrete areas instead of being intricately mixed as in the foregoing Malaita plot. Here the V.D.R. was zero for both *Anoplolepis* and *Occophylla* palms, as compared with 91·0 for those occupied by *Iridomyrmex*.

An instance of nutfall associated with Anoplolepis.—Of all the many plantations in which *Anoplolepis* was well represented, an important degree of nutfall was found associated with this ant in only one. This was the small plantation of Soso (Vatilau) in the Nggela group; *Iridomyrmex myrmecodiae* was the dominant ant here (occupying 50 per cent. of the palms), but *Anoplolepis* was also well represented (occupying 33 per cent. of the palms). Nutfall occurred in association with both these ants; figures obtained from sampling were as follows:—

	Iridomyrmex palms	*Anoplolepis* palms
V.D.R.	97	64
Crop average (nuts per palm per annum)	2	8

Although nutfall was severe in the *Iridomyrmex* palms, it was still considerable in those occupied by *Anoplolepis*. There was no obvious explanation of this, but the crowns of the palms were not examined, and it is not advisable to allow this isolated instance to affect the general conclusion that *Anoplolepis* protects palms against *Amblypelta*. There may be some simple, unrecognised local factor which affected the situation (see p. 125).

On the whole, the evidence from miscellaneous plots and samples indicates that *Anoplolepis*, when well established, gives nearly if not quite as much protection as does *Occophylla* against *Amblypelta* attack, although in some cases it tends to be associated with somewhat inferior crops. Possible reasons for this have been given, and suggest that this difference may not be due to any difference in the direct or indirect activities of the two ants.

(*e*) *Evidence from the behaviour of* Anoplolepis *in presence of* Amblypelta.

The manner in which *Anoplolepis* protects a palm against *Amblypelta* is of obvious interest. It is virtually impossible to observe under completely natural conditions, because the two insects are very rarely found in association. Even in heavy nutfall areas, associated with *Iridomyrmex* or *Pheidole*, usually no more than two or three individuals of *Amblypelta* are to be found on each palm, and often none are seen by climbers. The chances of finding *Amblypelta* on palms occupied by *Anoplolepis* are extremely remote.

Occasionally, *Anoplolepis* and *Amblypelta* are found in association on *Manihot esculenta* (cassava), an important alternative food-plant of *Amblypelta*. The ant only frequents this plant in small numbers, however, and the conditions cannot be regarded as similar to those in the crown of a coconut palm in which *Anoplolepis* is well established. On one occasion in Hulo Village (Malaita), an adult of *Amblypelta* on cassava was attended by one or two individuals of *Anoplolepis*, which walked round it and appeared to be "nibbling" at its legs. Every now and then the bug would jerk away slightly, and was obviously disturbed by the ants. On another occasion, however, near Honiara, three adults of *Amblypelta* were feeding on one cassava plant, on which there were also five or six individuals of *Anoplolepis*; occasional contacts were made between the ants and the bugs,

but the latter never seemed unduly disturbed. Hitherto, no immature individuals of *Amblypelta* have been found on cassava inhabited by *Anoplolepis*.

It is obvious that only observation on coconut palms can be really relevant. Phillips records that in 1936 he caged some individuals of *Amblypelta* on a coconut spadix in an *Anoplolepis* area at Karikana Estate, on Kolombangara. He states (*in litt.*) that " they were immediately killed by these ants ". Recently, at Kukum, the author repeated this experiment under the following circumstances.

A cage of mosquito netting was constructed, supported on a wire frame and large enough to enclose a complete spadix of young nuts (Pl. III, fig. 4). It was placed over a spadix, from which the male flowers had not yet fallen, on a palm with a strong *Anoplolepis* population. The open base of the netting was tied round a collar of bamboo tubes, which had previously been tied round the stem of the spadix; the tubes were large enough to permit the passage of *Anoplolepis* workers, but not of *Amblypelta*. Some individuals of *Amblypelta* were then introduced through the upper end of the cage, which was then closed. To begin with, five adults and five nymphs were introduced at about 11.30 a.m. There were at this time two or three dozen individuals of *Anoplolepis* on the spadix, and it was a long time before they made contact with the bugs, most of which remained on the walls of the cage for some time. By about 3.30 p.m. some contacts had been made; the numbers of ants in the cage had increased greatly; one adult bug had been killed and was being carried off by several ants, which had removed five of its legs; another adult bug was in process of being killed. Five more adults and five more nymphs were introduced; within ten minutes, three nymphs and two adults had been overpowered, each by about 6–10 ants which caught hold of its legs and rendered it powerless. The adults, being more active, were attacked more vigorously by the ants which became very excited by the struggles of the bugs, and ran round them at high speed seeking a hold for their jaws. At the same time, the adults were somewhat less vulnerable since they could escape by flight, often carrying one or more ants with them. Had the cage not been there the majority of them would probably have escaped. The nymphs, being sluggish, attracted less attention, and were often not attacked, but when they were, they put up very little struggle in self-defence.

By the next morning, only one adult and two nymphs survived out of a total of ten adults and ten nymphs introduced on the previous day. Ten more of each were then added; by the end of the day five adults and seven nymphs survived. The next morning only two adults, but all the seven nymphs were still alive; four more adults were added during the day, and by 3.15 p.m. four adults survived and six nymphs. The next morning two more adults had been killed, and four more adults and four nymphs were added. The cage was then left for two days, after which two adults and six nymphs remained. Thus over a period of five days a total of 28 adults of *Amblypelta* and 24 nymphs had been introduced into the cage, and at the end of the period 26 adults and 18 nymphs had been destroyed.

We may deduce from the experiment that the severity of the attack is greatest against the adults, the nymphs tending to survive better since they attract less attention owing to their sluggish habits. It is true that in the natural state most of the adults would probably escape with their lives, but the disturbing effect of the ants would be very great. When feeding, normally, a bug may remain in one position for as much as 40 minutes without withdrawing its stylets. Attack by *Anoplolepis* would therefore prevent normal feeding, since the bugs would not be left in peace for many seconds. For the same reason, breeding activities would be impossible on a palm strongly held by *Anoplolepis*, and *Amblypelta* could therefore never build up a population in an area occupied by this ant.

Any damage to the coconut crop would therefore be the result of the chance arrival by flight of adults from neighbouring areas, which might occasionally have time to feed for a short while before being attacked; such damage would be very

slight. It is important to realise, however, that *Anoplolepis* would have to be present in sufficient strength (as it usually is in an area with a continuous population) in order to bring about adequate protection. These considerations are therefore in agreement with the evidence derived from other sources concerning the relation between *Anoplolepis* and nutfall.

Other Species of Ants and their Relation to Nutfall.

A list of 35 species of ants recorded from coconut plantations in the Solomon Islands has been given by O'Connor (1950, p. 42). During the course of the present work, 65 species have been recorded (see Appendix B, p. 132) from plantations; this list includes all O'Connor's species except 12 (*Ponera pruinosa* (Emery), *Pheidolacanthinus belli* (Mann), *P. fusescens* (Emery), *Monomorium pharaonis* (L.), *M. fraterculus* Santschi, *Monomorium* spp. (2), *Oligomyrmex viehmeyeri* Mann, *Camponotus sanctae crucis* Mann, *C. belli* Mann, *C. ? chloroticus* (Emery), *Polyrhachis guerini* (Roger); of these, *Monomorium pharaonis* was found by the writer frequently, but not in coconut plantations, and it cannot be considered as typically a plantation species.

To judge from the long list of Solomon Islands species given by Mann (1919), a great many more could probably be found in plantations; but in all these lists only a few species are represented on an important scale; of those in Appendix B, apart from the four species of major importance already discussed, only the following are numerous enough to be considered from the point of view of any relation they may have to nutfall:—*Odontomachus haematodes* (L.), *Pheidole oceanica* Mayr, *P. umbonata* Mayr, *Pheidolacanthinus sexspinosus* (Mayr), *Monomorium floricola* (Jerd.), *Irenidris myops* Donisthorpe, *Iridomyrmex anceps* Roger ssp. *papuana* Emery, *Technomyrmex detorquens* (Wlk.), *Tapinoma melanocephalum* (F.), *Bothriomyrmex pusillus* (Mayr), *Paratrechina manni* Donisthorpe, *P. minutula* (Forel) ssp. *atoma* Forel, *P. vividula* (Nyl.) (with *P. vaga* Forel), *Camponotus irritans* (F.Sm.) var. *samoaensis* Santschi, *C. reticulatus* Roger var. *bedoti* Emery, *Polyrhachis salomo* Forel.

Paratrechina vividula and *P. vaga* are considered together because they are difficult, if not impossible, to distinguish, especially in the field, and the complex appeared to be ecologically homogeneous.

None of these "minor" species is ever dominant over large areas of plantation, as are the major species *Occophylla*, *Anoplolepis*, *Pheidole megacephala* and *Iridomyrmex myrmecodiae*. They only become common locally, usually in a zone between areas occupied by different major species, where one of the latter is in process of replacement by another. Occasionally, under such conditions, neither of the major species is in sufficient numbers to dominate the situation, and one or more (often several) of the minor species is enabled temporarily to become numerous. It is from such areas, therefore, that evidence of their relation to nutfall has to be collected. Rua Vatu plantation, on Guadalcanal, was in such a condition during the years 1954–56; it had been largely dominated by *Pheidole megacephala* for some years and had been suffering from severe nutfall, but this ant was rapidly disappearing and being replaced ultimately by *Occophylla*; other minor species were becoming locally common in the transition zone. It is largely from this plantation that the following data are taken.

It should be realised that such an area is in a condition of instability, and that the species of ant in occupation of a palm at any one time may not necessarily have been there for long. Therefore the crop of mature nuts associated with it, which was determined by the extent of *Amblypelta* attack some months previously, may be the result of occupation by some other species of ant. Conclusions from individual crop observations are therefore not reliable, although if they are based on a sufficient number of palms they are bound to include a fair proportion that have been occupied by the ant in question for some months, so

that the figures give some indication. Data obtained from vidaka damage rates are more reliable because they refer to a period of only two or three weeks previous to the observations.

The data obtained are given in Table VII. Although the species of ants concerned often occurred very commonly, only those palms are included on which

TABLE VII.

Crop estimates and vidaka damage rates for palms dominated by the more important of the " minor " species of ants.

	Oecophylla smaragdina	*Iridomyrmex myrmecodiae*	*Pheidole megacephala*	*Technomyrmex detorquens*	*Bothriomyrmex pusillus*	*Pheidole oceanica* *Pheidole umbonata* *Pheidolacanthinus sexspinosus*	*Paratrechina minutula* ssp. *atoma* *Paratrechina manni* *Paratrechina vividula* (incl. *P. vaga*)	*Camponotus irritans* var. *samoaensis* ; *Camponotus reticulatus* var. *bedoti*	*Polyrhachis salomo*	*Odontomachus haematodes*
No. of palms ..	1765	742	1059	449	225	50	77	24	26	88
Average crop (nuts/palm/annum)	56	23	21	31	19	31	34	34	36	31
Total fallen nutlets	1347	991	1845	391	482	87	84	10	15	63
V.D.R.	8·9	79·0	80·0	59·9	63·1	55·2	72·6	50·0	33·3	15·9

they were dominant to any others on the same palm. Where insignificant figures are available for a species individually, the latter have been combined where possible into groups of species that are closely related and have an apparently similar ecology. Also included in the Table are figures for the protective ant *Oecophylla* and the non-protective ants *Iridomyrmex myrmecodiae* and *Pheidole megacephala*, taken from the same areas of plantation as those for the minor species; thus the figures for the latter can be compared with those for a protective ant, with virtually no damage, on the one hand, and with ants associated with damage by *Amblypelta* approaching the maximum on the other.

It will be seen from the Table that not one of the minor species gives complete protection against nutfall. It is, in fact, doubtful whether they afford any protection at all; for although, in nearly all cases, the associated crop estimates are greater, and V.D.R. values less, than in the case of *Iridomyrmex myrmecodiae* and *Pheidole megacephala*, this is almost certainly because, the areas concerned being in a state of transition, a proportion of the palms may have recently been under the protective influence of *Oecophylla*. It is even possible that this ant was present, but unobserved, in the crowns of a small proportion of palms at the time of observation. The highest, and therefore most significant, numbers of observations available are for *Technomyrmex detorquens* and *Bothriomyrmex pusillus*, and the V.D.R. values associated with these may be regarded as fairly typical for transition species.

For purposes of discussion, the minor species included in the Table can be grouped as follows:—

(1) *Technomyrmex detorquens*
Bothriomyrmex pusillus
These two common species are usually to be found at the bottom of the trunk, but often, where they are very numerous and there are creepers on the trunk to provide protected runways, they may forage up to the crown, and then make direct contact with the spadices. The high values of the V.D.R. and the reduced crops are therefore indicative of their inability to give direct protection against *Amblypelta*.

(2) *Pheidole* spp. (except *Ph. megacephala*)
Pheidolacanthinus sexspinosus
Paratrechina spp.
These ants are almost invariably confined to the base of the trunk, except occasionally *Paratrechina manni*, and therefore rarely, if ever, make contact with the spadices. Their effect upon *Amblypelta* cannot therefore be direct.

(3) *Camponotus* spp.
Polyrhachis salomo
These species are almost invariably associated with other ants on coconut palms, even though they may occasionally be dominant. One colony usually covers an area containing several palms, especially in the case of *Camponotus reticulatus* and *Polyrhachis salomo*; the ants forage in a somewhat irregular manner on the palms within their territory, but seldom over the spadices. *Camponotus irritans* (which incidentally bears a superficial resemblance to *Oecophylla* and can be mistaken for it) usually inhabits nests in crevices on the trunk from which it seldom emerges except when disturbed. None of these ants, therefore, has any appreciable direct effect upon *Amblypelta*, and to this extent they resemble the species in group 2. There are several other species of *Polyrhachis* which occur under similar circumstances to *P. salomo*, but the latter is much the most common and widespread.

(4) *Odontomachus haematodes*
This is a ground-living ant invariably confined to the bases of the trunks. Owing to its large size and aggressive habits it may have some considerable indirect effect locally by preventing the access of other species to the palms.

Of the species listed at the beginning of this section, four have not been included in Table VII because the figures available are insufficient for analysis. This is because, although locally common, they are nearly always associated with other ants and are rarely dominant. *Monomorium floricola* is one of the commonest ants on coconut palms; it is small, and occurs on a large proportion of palms, even in association with the major species. Although it usually inhabits the crown, it is mainly confined to crevices such as the spaces between spadix sheaths; it rarely forages on the spadices themselves, and even when it does it is too small and insignificant to have any effect on *Amblypelta*. *Irenidris myops* and *Tapinoma melanocephalum* are also small and insignificant, and the former is always confined to the base of the trunk. *Iridomyrmex anceps* is larger and may forage right up to the palm crowns; however, it has never been found dominant in nutfall areas, and its relation to nutfall cannot be assessed.

To summarise, one may state that, so far as available evidence goes, the minor species of ants do not give any appreciable direct protection against *Amblypelta*, and any effect they may have is almost entirely indirect, by the exclusion

of other species. The fact that they are usually associated with slightly better crops and lower vidaka damage rates than are *Pheidole megacephala* and *Iridomyrmex myrmecodiae* may be attributed to the fact that they are usually only common in transition areas with an unstable but very varied ant population, where the influence of protective species, though slight, is none the less appreciable.

The Distribution of *Amblypelta* Species and its Relation to Nutfall.

The distribution and local status of nutfall is primarily dependent on that of the species of *Amblypelta*, which, so far as known at present (Brown, 1958*a*), is as follows (see fig. 2):—

1. No species present	Russell Is. Ontong Java
2. *Amblypelta gallegonis* Lever	
subsp. *gallegonis* Lever	Ysabel
subsp. *bougainvillensis* Brown	Choiseul, Bougainville
3. *Amblypelta costalis* Van Duzee	
subsp. *costalis* Van Duzee	Bellona
subsp. *rennellensis* Brown	Rennell
4. *Amblypelta cristobalensis* Brown	San Cristobal
5. *Amblypelta cocophaga* China	
subsp. *cocophaga* China	Guadalcanal, Nggela, Western Islands (except Choiseul), Bougainville
subsp. *malaitensis* Brown	Malaita

Arranged in this manner, the islands or groups of islands are, approximately, in increasing order of severity of nutfall.

Group 1.

Nutfall is absent from the Russell Islands and Ontong Java because *Amblypelta* does not exist there.

Group 2.

A. gallegonis only rarely attacks coconuts, or possibly not at all. Consequently nutfall has never been recorded on Ysabel, where *A. gallegonis* is the only species known to occur. On Choiseul and Bougainville, nutfall is of very restricted occurrence and not important, although it was found by the writer and Dr. J. J. H. Szent-Ivany at Numa-Numa on Bougainville, and by Mr. P. G. Fenemore at Luti on Choiseul. *A. gallegonis bougainvillensis* is plentiful on both islands, and, on Bougainville, *A. cocophaga cocophaga* has been found as well (although it appears to be relatively scarce). It has not yet been established which species of *Amblypelta* causes the nutfall on these two islands; it may be that *A. cocophaga* occurs sparingly on Choiseul as well as Bougainville, and is responsible. On the other hand, it is possible that *A. gallegonis bougainvillensis* does occasionally attack coconuts. At Numa-Numa some were caged with young coconut spadices, and they did in fact feed on the young nuts, but only in a half-hearted manner and not as readily as *A. cocophaga* does under similar circumstances; it was as if they only fed on coconut because nothing else was available. One can safely conclude that if *A. gallegonis* does feed on coconut it


FIG. 2. BRITISH SOLOMON ISLANDS AND BOUGAINVILLE.
Showing Distribution of Immature Nutfall and Amblypelta Species.
Scale of Miles
0 50 100 200
Nutfall—
Indicates heavy or extensive nutfall
Indicates light or restricted nutfall
Species of Amblypelta—
Amblypelta cocophaga
Amblypelta gallegonis
Amblypelta cristobalensis
Amblypelta costalis
Buka
Numa-Numa
BOUGAINVILLE
Shortland Is.
Ontong Java (Lord Howe Atoll)
Roncador Reef
CHOISEUL
Luti
Vella Lavella
Kolombangara
Vangunu
Gizo
NEW GEORGIA
Rendova
Tetipari
YSABEL
Gatare
Gossuru
Fara Is.
Fulakora
RUSSELL IS.
Sikiana
Auki
NGGELA
MALAITA
Soso
Baurani
Mamara
Tanavu
Rua Vatu
Kaukau
Marauna
Marau
Ulawa
GUADALCANAL
Malu Bay
Ugi
Three Sisters
Hauhaimarai
Bulimaterava
SAN CRISTOBAL
Santa Anna
Santa Catalina
SANTA CRUZ
Bellona
RENNELL
Vanikoro
155°
160°
165°
6°
8°
10°
12°

Fig. 2.

does so only occasionally and is unlikely to be a serious pest; more favoured food-plants have already been indicated (Brown, 1958*b*).

Group 3.

A. costalis is, like *A. gallegonis*, not strongly attached to coconut and much prefers *Manihot esculenta*, so that Rennell and Bellona only suffer slightly from nutfall. Values of the V.D.R. in the few localities where nutfall occurred at all, varied from 3 to 53, with an average of 25, and this in spite of the apparent absence of the protective ant, *Occophylla*. This low incidence of insect damage did not appear to reduce crops at all seriously, although the effect was difficult to estimate owing to the extensive gathering of green coconuts by the natives for drinking, which reduced the number of nuts on the palms.

Group 4.

Amblypelta cristobalensis has only recently been distinguished from *A. cocophaga* (Brown, 1958*a*); it is confined to the island of San Cristobal, where it is apparently the only species present. Although it has not actually been taken on coconuts, there is no room for doubt that it is the species responsible for nutfall on this island. The nutfall is not serious as a whole, being very restricted in distribution, although it is severe in certain very limited areas. Out of 16 European-type plantations examined, nutfall was found to occur in only five.

There is an interesting feature in which nutfall on San Cristobal differs from that on Malaita, Nggela and Guadalcanal; namely, that what nutfall there is, occurs almost exclusively in association with *Pheidole megacephala* rather than *Iridomyrmex myrmecodiae*, although the latter ant is well represented in several plantations. This is made clear from the following list of plantations on San Cristobal and the adjacent small islands, where all the important European-type plantations and some village groves were examined; a + indicates the presence of the ant in question, and "n" indicates that nutfall was associated with it, the value of the V.D.R. being in this case shown afterwards in brackets.

Plantation	*Iridomyrmex* present	*Pheidole* present
Anchor Is.	+	—
Boroni	+	+ n (68)
Bulimaterava	+	+ n (91)
Hawa	+ n (46)	—
Maru	+	+
Maru Bay	+	+
Pawa	—	+
Santa Anna	+	+
Sungasau	—	—
Su'umoli	+	—
Three Sisters	+	—
Waiai	+	—
Waimamura	+	—
Waimarai	+ n (?)	+ n (84)
Waimasi	+	—
Wainoni	+	—
Ahia	+	+
Kelimei	+	—
Santa Catalina	+	—
Taranigogofani (Santa Anna)	—	+
	17	9

It can be seen that while *Iridomyrmex* occurred in 17 plantations and *Pheidole* in only nine, nutfall was found associated in four cases with *Pheidole* and only

in two with *Iridomyrmex*; furthermore, the nutfall was more severe when associated with *Pheidole*.

One small plantation of about 60 acres (Maru Bay) was of particular interest in this connection.

The northern end of the plantation was occupied by a pure colony of *Pheidole megacephala*, and suffered from severe nutfall. A nymph of *Amblypelta* was found at the foot of one palm, having probably fallen from the crown. Towards the southern end, the plantation grows wider; here, *Pheidole* gives place to *Oecophylla* and *Anoplolepis* in the coastal part, and to *Iridomyrmex* in the inland part; in neither of these areas is there any nutfall, and crops are good. Figures obtained from samples are as follows:

	Pheidole	*Iridomyrmex*	*Oecophylla* and *Anoplolepis*
V.D.R.	$\frac{335}{386} = 89$	0/38 = 0	0/70 = 0
Crop (nuts/palm/annum) ..	7·6	68	73

Evidently in this plantation *Amblypelta cristobalensis* attacks palms with *Pheidole*, but not with *Iridomyrmex*; since the areas occupied by these two ants are adjacent, it is very unlikely that this is due to pure chance.

In an adjacent village grove (Ahia village), although there was a great predominance of non-protective ants, no nutfall was found (V.D.R. 0/124 = 0). In a sample of 75 palms traversing the grove from sea-level up the hill-side behind the village, the four major ant species occurred in the following numbers:

Iridomyrmex	42	49
Pheidole	7	
Anoplolepis	13	19
Oecophylla	6	

With such a preponderance of non-protective species, one would certainly expect nutfall; its absence may be due to the preponderance of *Iridomyrmex* over *Pheidole*.

In the only two plantations where nutfall occurred in association with *Iridomyrmex*, it was not severe. At Hawa, nearly half the plantation was occupied by this ant, but the V.D.R. was only 46, and the crops averaged 40 nuts/palm/annum, so that the effect was not very serious. At Waimarai, the V.D.R. was not recorded, but crops averaged 56 nuts/palm/annum for *Iridomyrmex* palms as compared with 35 for *Pheidole* and 71 for *Oecophylla*.

The reason for the very marked difference in the relations of *Pheidole* and *Iridomyrmex* to nutfall is not at all clear. It may be due to some difference in the behaviour or vigour of the ants on these as compared with other islands, but since *Iridomyrmex* is widespread and probably homogeneous in habits over its range, it is more likely to be due to differences in the nature of *Amblypelta cristobalensis*, such that *Iridomyrmex* can give relatively more protection against it than it can against *A. cocophaga*. Even on other islands, it is usually found that *Pheidole* areas suffer more severely from *Amblypelta* attack than do *Iridomyrmex* areas.

Group 5.

Of all the known species of *Amblypelta*, *A. cocophaga* China (including both its subspecies) appears to be the most strongly attached to coconut, and the worst nutfall is therefore found in the islands where it occurs, namely Malaita (subsp. *malaitensis* Brown), Guadalcanal, Nggela, and, in the Western Islands of New Georgia, Kolombangara and a few others (subsp. *cocophaga* China). *A. cocophaga* has been collected on Bougainville, but seems to be scarce, and nutfall is very limited, being apparently confined to Numa-Numa plantation (see under Group 2, above, for a discussion of the status of nutfall on this island and on Choiseul).

In estimating the losses due to nutfall in the different islands of this group, only European-type plantations will be taken into account. For each plantation an approximate estimate was obtained as follows. First, the fraction of the plantation suffering from nutfall was estimated as far as sampling data allow; then, by comparison of the crops in nutfall areas with those in adjacent protected areas, the fraction of the potential crop which is lost in the nutfall areas was calculated. The product of these two fractions then represents the fraction of the total crop lost in the plantation as a whole. This system is subject to certain sources of error. Most important, owing to the limited time available, the samples in many cases did not cover a plantation sufficiently well, and thus may not have been truly representative. Secondly, the method of crop estimation on which the extent of damage caused by *Amblypelta* is based is open to criticism (see Appendix A); it should be noted that the system of crop estimation, by tending if anything to under-estimate higher crop grades, may in some cases result in a corresponding underestimate of the fraction of the crop lost through nutfall. Moreover, it was frequently impossible to obtain data of the planted acreage of a plantation, or of a whole island, and details of annual production over a period of years were rarely obtainable. For these reasons it was found impossible to give an even approximately accurate figure for the losses due to nutfall in the islands as a whole.

The status of nutfall in the islands of Group 5 as indicated in the manner described is shown in Table VIII. It will be seen that, on Malaita, six out of nine plantations lose half or more of their crops through nutfall, the remainder losing only slightly less than half. Nutfall is thus very serious on Malaita. Nggela comes next in order in degree of damage, so far as the only two European-type plantations are concerned; native groves have not been recently studied on this island, but are said to suffer badly, and it is possible that Nggela loses over half its total copra through nutfall.

Guadalcanal suffers far less acutely at the present time. Of the European plantations examined, nutfall has been found at Berande, Kau-Kau, Kukum, Lunga, Mamara, Marau, Maraunia, Rua Vatu and Tenaru; it has not been found at Aruligo, Ivatu, Rere, Rua Sura, Symon Is., and Tetere, except in minute traces at Aruligo and Rere. It is of little importance at Kukum, Lunga, Marau, and probably Berande, so that only Kau-Kau, Mamara, Maraunia, Rua Vatu and Tenaru suffer at all severely; for these five together, about 25 per cent. would be a fair estimate for the proportion of nuts lost due to *Amblypelta*. This figure, however, is based on the assessment of Rua Vatu as it existed in 1953; if its present rate of recovery continues the loss will soon be very much less. Guadalcanal at present does not therefore present a serious nutfall problem as it used to before the war; the improvement is undoubtedly due to large-scale changes in the ant population, first in the Kukum-Lunga-Tenaru plantations and more recently at Rua Vatu.

The Western Islands if anything suffer even less than does Guadalcanal, for although crops are very poor in many of the plantations, this is seldom due to *Amblypelta*, but rather to a combination of poor soils and lack of proper

TABLE VIII.

European-type plantations examined in Malaita, Guadalcanal, Nggela and the Western Islands, showing (where possible) approximate estimates of the proportion of crops lost through attack by *Amblypelta cocophaga*.

Island and plantation	Planted acreage (when known)	Fraction of plantation with nutfall	Fraction of crop lost in nutfall area	Approximate fraction of crop lost for whole plantation
MALAITA				
Baunani :				
Kwa	—	7/18	24/25	3/8
Manaba	—	2/3	69/75	3/5
Hulo	—	12/19	23/31	1/2
Baunani	—	5/12	9/10	3/8
Assimana	—	17/29	3/4	1/2
Igua	—	3/5	3/4	1/2
Su'u	—	1	1	1
Ba-Ekwa Is.	—	1	1	1
Buma	—	1/3	?	1/3
NGGELA				
Mandoliana	—	0	0	0
Soso	—	1	13/14	13/14
GUADALCANAL				
Aruligo	—	0	0	0
Berande	—	1/5	1/3	1/15
Ivatu	250	0	0	0
Kau-Kau	906	2/7	14/25	1/6
Kukum (with Lunga and Tenaru)	2470	1/30	1/2	1/60
Mamara	—	1/2	1/2	1/4
Marau	—	1/20	2/3	1/30
Maraunia	—	1/3	6/7	2/7
Rere	1000	1/100	2/3	1/150
Rua Sura	300	0	0	0
Rua Vatu (in 1953)	946	3/4	1	3/4
Symon Is.	—	0	0	0
Tetere	—	0	0	0
THE WESTERN ISLANDS				
Arundel	—	0	0	0
Gizo :				
Loga Is.	—	0	0	0
Nusabaruku	—	0	0	0
Kolombangara :				
Karikana	—	?	?	?
Lady Lever	—	1/11	12/49	1/45
Stanmore	—	0	0	0
New Georgia :				
Banga	—	0	0	0
Pauru	—	1/4	1/2	1/8
Rendova :				
Rendova	—	1/50	?	1/50
Kokorana Is.	—	1/25	4/9	1/56
Tetipari :				
Waugh Bay	—	1/30	2/3	1/45

maintenance during and after the war. The only plantation where *Amblypelta* nutfall is now conspicuous is Karikana on the island of Kolombangara. The reason for the comparative freedom from attack in the Western Islands is far from clear, since *Pheidole* and *Iridomyrmex* are quite well represented. It may be connected with the overgrown condition and consequent complexity in ant populations, but this is highly conjectural and it is impossible to prophesy what effect rehabilitation and maintenance would have on nutfall.

In Table IX the status of nutfall on San Cristobal and the adjacent small islands is shown in a similar manner for comparison; it can be seen that in only

TABLE IX.

European-type plantations examined in San Cristobal and adjacent islands, showing approximate estimates of the proportion of crops lost through attack by *Amblypelta cristobalensis*.

Plantation	Planted acreage (when known)	Fraction of plantation with nutfall	Fraction of crop lost in nutfall area	Approximate fraction of crop lost for whole plantation
Anchor Is. ..	—	0	0	0
Boroni	—	1/100	4/9	1/225
Bulimaterava ..	—	1/20	1/12	1/250
Hawa	153	1/2	11/51	1/9
Maru	—	0	0	0
Maru Bay ..	60	1/2	9/10	1/2
Pawa	—	0	0	0
Santa Anna ..	—	0	0	0
Sungasau ..	—	0	0	0
Su'umoli	—	0	0	0
Three Sisters ..	962	0	0	0
Waiai	150	0	0	0
Waimamura ..	343	0	0	0
Waimarai ..	—	2/3	1/2	1/3
Waimasi ..	—	0	0	0
Wainoni	—	0	0	0

two plantations (Maru Bay and Waimarai) is there a really substantial fraction of the crop lost; and these two plantations are both small.

The variation in intensity of nutfall on the different islands within the range of *Amblypelta cocophaga* is striking; on Malaita it is high, and also on Nggela; on Guadalcanal it is relatively low, and in the West lower still (comparable with the condition on San Cristobal). In view of the obvious differences between species of *Amblypelta* with regard to their attachment to coconut, it is tempting to suppose that there are subspecific and local population differences within *A. cocophaga* as regards the same character. The Malaita subspecies *malaitensis* Brown is taxonomically very distinct and may well be also more attached to coconut. It has also been pointed out (Brown, 1958*a*) that there are colour differences in the Western Islands population of subspecies *cocophaga* and there may also be a difference in attachment to coconut. There may also be differences in resistance to *Iridomyrmex myrmecodiae*, associated with which nutfall is more intense on Malaita than on some of the other islands (contrast the condition with *A. cristobalensis* on San Cristobal, described above (p. 121). A similar variation in resistance to *Anoplolepis longipes* may possibly account for the fact that this ant, which in all other islands protects the palms from *Amblypelta*, was found associated with nutfall on Nggela (p. 114). This is only conjectural, but is put forward as a possible explanation of instances of local variation in intensity of

nutfall which are not obviously related to ant distribution. It perhaps gains some support from the fact that, in Zanzibar, *Anoplolepis longipes* apparently gives no protection against *Pseudotheraptus wayi* (Way, 1951), which causes nutfall there (Way, 1953), although this Coreid is closely related to *Amblypelta cocophaga* and comparable with it in size and general characteristics.

Further Considerations in Assessing the Extent of Losses through *Amblypelta* Attack.

In the foregoing pages a system for assessing losses has been used, based on estimations of crops in areas of nutfall and comparing them with crops in adjacent areas not suffering from nutfall. The crop estimation is based on the number of nuts on the palm, and thus indicates the direct damage by the insect in terms of the deficiency in the number of nuts that survive to maturity. This assessment of damage is minimal, because it does not take into account two further factors that can be important. These are discussed below.

(*1*) *Loss of copra in surviving nuts.*

In areas of moderate nutfall, a varying number of nuts survives attack by *Amblypelta* and grows to maturity, but many retain feeding scars caused in the early stages and are distorted and stunted to varying degrees according to the extent of the attack and the stage of growth at which it took place. This results in a corresponding reduction in the yield of copra from these nuts: in a small proportion of those more heavily attacked the endosperm fails to develop and rots, resulting in complete loss of the copra. In order to arrive at a correct estimate of loss in copra, that due to this factor must clearly be added to the reduction in the number of whole nuts that reach maturity.

In two areas of moderate nutfall occupied by *Iridomyrmex*, at Kukum and Tenaru on Guadalcanal, estimates were made of the percentage of copra lost in this way. All the fallen mature nuts were collected from a limited area in each locality, and they were sorted into six classes as follows:—

Class 1: without scars
Class 2: with 1–5 scars
Class 3: with 6–20 scars
Class 4: with more than 20 scars, in a single ring round the nut
Class 5: with more than 20 scars distributed more or less all over the nut
Class 6: heavily scarred nuts in which the endosperm has failed to develop.

The difference between classes 4 and 5 depends on whether the nut has been attacked once only during its development (class 4), or repeatedly (class 5), resulting, respectively, in lesser and greater reduction of copra. Examples of nuts of classes 2–5 are illustrated in Plate II, fig. 3.

Within each class, the "green" copra was extracted from the nuts and weighed, the copra from aggregates of five nuts being placed together for this purpose. The average weight of green copra per nut (in grammes) was then calculated for each of the five classes, and the following figures were obtained:—

	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6
Kukum	381	343	317	252	247	0
Tenaru	368	355	302	279	260	0

A fairly close agreement will be seen in the two sets of figures. If the class 1 figures are taken as the average potential weight for an undamaged nut for the

locality, the loss due to *Amblypelta* for each of the other classes can be found by subtracting the average weight from the class 1 figure.

If the number of nuts by which each class is represented in the total sample is taken into account, then the total loss of copra can be calculated. The figures for the two areas concerned are shown in Table X.

TABLE X.

Loss in weight of copra in mature nuts in two areas of moderate nutfall at Kukum and Tenaru on Guadalcanal.

		Class 1	Class 2	Class 3	Class 4	Class 5	Class 6
Kukum	No. nuts in each class in sample of 515	253	150	57	36	11	8
	Av. loss in wt. per nut (g.)	0	38	64	129	134	381
	Total loss for all nuts (g.)	0	5,700	3,648	4,644	1,474	3,048
	Total potential wt. (381 g. per nut)	515 × 381 = 196,215 grammes					
	Total loss (Classes 2–6)	18,514 grammes					
	% loss in wt.	9·4					
Tenaru	No. nuts in each class in sample of 366	164	97	75	15	10	5
	Av. loss in wt. per nut (g.)	0	13	66	89	108	368
	Total loss for all nuts (g.)	0	1,261	4,950	1,335	1,080	1,840
	Total potential wt. (368 g. per nut) ..	366 × 368 = 134,688 grammes					
	Total loss (Classes 2–6)	10,466 grammes					
	% loss in wt.	7·8					

If these two examples are representative of areas of moderate nutfall throughout the islands, then we can assume that surviving nuts in such areas produce less copra, by a figure somewhat less than 10 per cent., than they would do if they had not been attacked by *Amblypelta*. This loss must therefore be taken into account in assessing the total losses due to *Amblypelta* attack. It is in fact probably subject to a greater range of variation than is indicated by these two samples only, and is likely to be greater where attack is more severe and damage to the nuts generally is more extensive.

(2) *Losses due to plantations not being worked.*

Large areas of coconuts, and even whole plantations, which are suffering from nutfall, are not infrequently not worked at all, because the crops are so reduced by *Amblypelta* that recovery of the copra that remains is not worth while. This is particularly true of plantations that inevitably fell into neglect during the war years, and which the owners have judged would not be worth the expense of rehabilitating. Such areas and plantations must be considered a total loss, even although the direct damage by *Amblypelta* may only destroy a proportion of the crops. In other areas (such as the large plantations at Baunani on Malaita),

nutfall is patchy, being severe in some parts and only moderate in others; the latter may be only partially worked, the nuts being collected but the plantations not being kept free from weeds and thick undergrowth; in such cases only a proportion of the mature nuts is collected, the remainder going to waste.

This is another factor that reduces copra production, and that needs to be taken into account when assessing losses due to *Amblypelta*, in addition to the estimates made by other methods. Insufficient data are available, however, to quote any figures indicating its importance.

Summary.

In the British Solomon Islands Protectorate, the incidence of the immature nutfall of coconuts that is caused by species of *Amblypelta* depends upon the distribution of (1) the species that are concerned, which determines on what islands nutfall occurs, and (2) certain species of ants, which affects the local distribution of nutfall on those islands. *A. cocophaga* China is the most important member of the genus as regards responsibility for nutfall; *A. cristobalensis* Brown and to a less extent *A. costalis* Van Duzee also frequent the coconut palm and cause nutfall, but not on a serious scale; *A. gallegonis* Lever rarely, if ever, attacks coconut.

The current view that *Oecophylla smaragdina* (F.) protects coconuts against *Amblypelta*, and that *Pheidole megacephala* (F.) and *Iridomyrmex myrmecodiae* Emery give little or no protection, is accepted, but evidence is brought forward showing that *Iridomyrmex* appears to give some protection against *A. cristobalensis* on San Cristobal. Most attention has been given to a fourth species of ant, *Anoplolepis longipes* (Jerd.), the relation of which to nutfall has hitherto been in some doubt; evidence from various sources shows that, at least on Guadalcanal and Malaita, it gives nearly, if not quite, as much protection against *Amblypelta* as *Oecophylla* does.

A method based on crop estimation is used to give some indication of the losses due to nutfall in the European plantations that have been surveyed. The accuracy of the method is discussed in an Appendix. Varying numbers of nuts survive to maturity in nutfall areas, depending on the intensity of attack. In addition to the loss caused by the failure of nuts to survive to maturity, *Amblypelta* attack causes further losses by reducing the amount of copra obtainable from surviving nuts, and by rendering plantations where the attack is sufficiently severe unprofitable to work, so that they become, in effect, a total loss, even though a proportion of the nuts may survive attack.

An attempt is made to evaluate and compare the fraction of the crop lost on some of the principal islands, but it is impossible to give an even approximately accurate figure for the losses due to nutfall in the islands as a whole, because essential data, comprising the planted acreage of each plantation and island, and, except for a very few plantations, details of annual production figures over a period of years, are often lacking; also, limited time has made it impossible to survey many of the plantations in sufficient detail for an accurate assessment of nutfall.

A list is given of the species of ants recorded from coconut plantations during the present work.

Acknowledgements.

I wish to express my deep gratitude to all those who have helped me in a variety of ways in this work; to Mr. D. A. Donald, the Senior Agricultural Officer of the British Solomon Islands Protectorate, and his staff; to Dr. W. J. Hall, C.M.G., Director of the Commonwealth Institute of Entomology and his staff for identifications of insects, and especially to Mr. G. E. J. Nixon for the

determination of numerous samples of ants; to the owners and plantation managers of coconut estates in the islands, and especially to the Managing Director of Messrs. Levers' Pacific Plantations Pty Ltd. and his staff, for their hospitality and providing assistance and facilities in all manner of ways for work in the plantations; and especially to Mr. A. H. Green, agronomist to Messrs. Levers' Pacific Plantations Pty Ltd., whose experience and knowledge of coconut plantations in the islands has been invaluable and freely given; to Mr. P. G. Fenemore for information about nutfall on Choiseul Islands, which I was unable to visit, and to Dr. J. J. H. Szent-Ivany for inviting me to accompany him on a survey of nutfall on Bougainville Island; and to my assistants L. V. Waibuta and K. Nui, whose help, especially in the field work, was both willing and able.

References.

Brown, E. S. (1958*a*). Revision of the genus *Amblypelta* Stål (Hemiptera, Coreidae).—*Bull. ent. Res.* **49** pp. 509–541.

Brown, E. S. (1958*b*). Injury to cacao by *Amblypelta* Stål (Hemiptera, Coreidae) with a summary of food-plants of species of this genus.—*Bull. ent. Res.* **49** pp. 543–554.

Mann, W. M. (1919). The ants of the British Solomon Islands.—*Bull. Mus. comp. Zool. Harv.* **63** pp. 273–391.

O'Connor, B. A. (1950). Premature nutfall of coconuts in the British Solomon Islands Protectorate.—*Agric. J. Fiji* **21** pp. 21–42.

Phillips, J. S. (1956). Immature nutfall of coconuts in the British Solomon Islands Protectorate.—*Bull. ent. Res.* **47** pp. 575–595.

Vanderplank, F. L. (1958). Studies on the coconut pest, *Pseudotheraptus wayi* Brown (Coreidae), in Zanzibar. I. A method of assessing the damage caused by the insect.—*Bull. ent. Res.* **49** pp. 559–584.

Way, M. J. (1951). An insect pest of coconuts and its relationship to certain ant species.—*Nature, Lond.* **168** p. 302.

Way, M. J. (1953). Studies on *Theraptus* sp. (Coreidae); the cause of the gumming disease of coconuts in East Africa.—*Bull. ent. Res.* **44** pp. 657–667.

Appendix A.

Crop Estimation.

In order to assess and compare the importance of nutfall in different areas, it is necessary to have a sound method of estimating crops. There are two obvious methods of doing this accurately, (1) by harvesting all the nuts from such areas over a period, and counting them or weighing the copra, (2) by counting all the nuts on each palm.

For much of the present work, and particularly for regional surveys, when it was important to estimate crops as rapidly as possible, neither of these methods was suitable; the first, because it requires observations over a long period, and the second because it takes too much time in the case of heavier crops, and is

difficult to carry out from ground-level, from which a number of nuts may be invisible.

A simplified form of the second method, however, was devised by R. Leach (unpublished report to Messrs. Lever Bros., 1948). In this method, estimation of higher crop grades is based on the number of nuts on each spadix. Usually about six or seven spadices with nuts full-grown or nearly full-grown can be seen on each palm from the ground, and most of them can usually be seen clearly enough to estimate the number of nuts on each fairly accurately. Leach was able to classify crops on this basis into five grades; with only minor modifications in the limits of his grade 1, the same system has been used in this work; the following grades have been recognised:—

Grade 0—No crop
Grade 1—1–5 nuts *per palm*
Grade 2—1–3 nuts *per spadix*
Grade 3—4–6 nuts *per spadix*
Grade 4—Heavy crop, more than 6 nuts *per spadix*.

This system of crop recording is convenient, and assessments can be made rapidly in the field, after a little practice; a sample of 100 palms can be graded in less than an hour. Illustrations on Plate III give an idea of the visible appearance of certain crop grades; figs. 1, 2, 3 and 4 illustrate grades 0, 2, 3 and 4, respectively.

Two refinements can be made in order to convey further detail about the condition of the crop:—

(a) The various spadices on one palm are often by no means homogeneous; some, for instance, may be of grade 2 and others of grade 3, or even 4. The range is therefore denoted in estimating the palm as a whole, *e.g.*, 2–3, 2–4, 3–4 and so on; if half the spadices are of grade 4 and the remainder only have one or two nuts between them, the crop may be expressed 1–4; judgment must be used, however; for instance, if five spadices can be seen of grade 2 and only one with four or five nuts on it (grade 3), then it is more accurate to reckon the crop as a whole as grade 2 rather than as grade 2–3. Thus we have finer gradations intermediate between Leach's standards; 2–3 may be expressed as $2\frac{1}{2}$, 2–4 as 3, 1–4 as $2\frac{1}{2}$, and so on.

(b) Where older (lower) spadices have crops plainly at variance with those of younger (upper) spadices, this is denoted by expressing the crop thus:— 4/2, 3/0, etc., indicating crop grades of 4 and 3, respectively, on upper and of 2 and 0 on lower spadices. This is often of great significance, for example when a palm has recently recovered from nutfall.

It is necessary to be able to translate the symbolic grade numbers into something more tangible, if we require to obtain average crop values for a sample or block of palms. Leach rated each grade in terms of the percentage it represents of the maximum potential crop, but this method is unsatisfactory since it is impossible to judge what is the "maximum potential crop" under any given conditions of soil and other factors besides *Amblypelta* attack. The following method, which appears to be sounder, has been used in the present work; it aims at translating grade numbers into number of nuts produced per annum.

If we assume that a palm produces 12 spadices in a year, it is a simple matter; *e.g.*, a palm of grade 2 produces 12 spadices each with 1–3 nuts (average 2), which means $12 \times 2 = 24$ nuts per annum; while a palm of grade 2–3 will produce, on average, 6 spadices with 1–3 (average 2) nuts, and 6 with 4–6 (average 5) nuts; *i.e.*, $(6 \times 2) + (6 \times 5) = 42$ nuts per annum. When translating grade 1, which concerns all the large-size nuts on the whole palm, it is necessary to assume that 6 or 7 spadices (or approximately half a year's crop), have full-grown or nearly full-grown nuts at any one time; thus the total number of visible large-size nuts is doubled to give the annual crop; or since the average

of 1–5 nuts is 3, grade 1 palms may be expected to produce 6 nuts per annum on average. Figures for all crop grades are thus as follows:—

Crop grade	Designation	Nuts per palm per annum	Interval
0	No crop	0	
			6
1	1–5 nuts per palm	6	
			9
1½		15	
			9
2	1–3 nuts per spadix	24	
			18
2½		42	
			18
3	4–6 nuts per spadix	60	
			18
3½		78	
			18
4	Over 6 nuts per spadix	96	

In calculating the average annual crop per palm for a whole plot or sample of palms, the total nuts produced by all added together is divided by the number of palms. It can be seen from the Table above that the intervals between grades are not even, except above grade 2. It is therefore incorrect first to average the crop grades for all palms and then express this average figure in terms of nuts per annum, although one could do this if all the palms were of grade 2 or higher. The grade number is thus of no value except in making the initial estimates in the field; for this purpose, owing to the speed with which estimates can be made, it is a very satisfactory system.

There are certain sources of error in this method of crop estimation:—

1. Nuts of different varieties of coconut vary greatly in size; *e.g.*, Malayan nuts are large, and Samoan small, and a full potential crop will consist of a smaller number of nuts per spadix for the former and a larger number for the latter. If we adhere strictly to the number of nuts per spadix, therefore, as the basis for grading, the same crop grade may mean different things in the two types, in terms of weight of copra and percentage of the full potential crop. This has, however, been taken into account in grading during the work described in this paper; *e.g.*, a spadix with 6 large nuts, representing obviously a full potential crop, has been reckoned as grade 4 although by definition it should come in grade 3.

2. It has been found by careful checking in certain cases that there is a tendency to under-estimate higher crop grades, for two reasons; first, because it is difficult to see and count all the nuts in heavily laden spadices; and secondly, because in very heavy crops of smaller types of nuts the number may be as high as 20 nuts per spadix, and even, in exceptional cases, over 30; thus grade 4 covers a very wide range, and when translating it into terms of nuts per palm per annum the figure 96 is often much lower than it should be. One result of this is that in assessing nutfall as the percentage loss of the full potential crop, the estimated loss is often less than it should be.

3. Translation of crop grade into terms of nuts per palm per annum is based on an average production of 12 spadices per palm per annum. It has been found, however, that this figure varies considerably, tending to be smaller in poorer crops and larger in heavier crops. This likewise results in underestimation of the heavier crops when expressed as nuts per palm per annum, and also in over-estimation of poorer crops.

The errors pointed out in (2) and (3) above have not been allowed for in the present work, and may be important in certain cases. Since most of the conclusions have been based on averages from large numbers of palms, however, the errors are not likely to be serious, but the tendency, mentioned above, to under-estimate losses due to nutfall should not be forgotten.

Appendix B.

List of Ants recorded from Coconut Plantations in the Solomon Islands.

(N.B., species marked with an asterisk were also recorded by O'Connor (1950).)

Ponerinae.

Rhytidoponera froggatti (Forel)
Euponera (*Trachymesopus*) *stigma* (F.)
Euponera stigma (F.) ssp. *quadridentata* (F.Sm.)
Ponera sp.
Leptogenys (*Lobopelta*) *diminuta* (F.Sm.) ssp. *santschi* Mann
**Odontomachus haematodes* (L.)
Odontomachus ?saevissimus (F.Sm.)
Anochetus punctiventris Mayr ssp. *oceanicus* Emery

Myrmecinae.

**Pheidole megacephala* (F.)
Pheidole nindi Mann
**Pheidole oceanica* Mayr
**Pheidole philemon* Forel
**Pheidole umbonata* Mayr
Pheidole sp.
**Pheidolacanthinus sexspinosus* (Mayr)
Pheidolacanthinus sp.
**Cardiocondyla nuda* Mayr
Crematogaster (*Rhachiocrema*) *abrupta* Mann
Crematogaster (*Acrocoelia*) *obnigra* Mann
Crematogaster (*Acrocoelia*) *?scita* Forel
Crematogaster (*Orthocrema*) sp.
Crematogaster sp.
Vollenhovia oblonga (F.Sm.) ssp. *pedestris* (F.Sm.)
Monomorium floricola (Jerd.)
Monomorium sp.
Diplomorium sp.
**Pristomyrmex* sp.
Rogeria sp.
**Tetramorium guineense* (F.)
Tetramorium simillimum (F.Sm.)
**Tetramorium tonganum* Mayr
**Strumigenys godeffroyi* Mayr
Strumigenys sp.
Ireneidris myops Donisthorpe

Dolichoderinae.

**Iridomyrmex myrmecodiae* Emery
Iridomyrmex anceps Roger ssp. *papuana* Emery

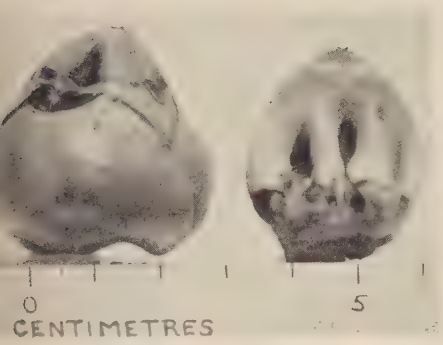
DOLICHODERINAE—*continued.*

**Technomyrmex detorquens* (Wlk.) (*T. albipes* (F.Sm.)) incl. var. *vitiensis* Mann
**Tapinoma melanocephalum* (F.)
Tapinoma timidum (Santschi)
Tapinoma sp.
Bothriomyrmex pusillus (Mayr)
Bothriomyrmex sp. nr. *flavus* Crawley
Bothriomyrmex sp.

CAMPONOTINAE.

Acropyga moluccana Mayr ssp. *papuana* Mann
Plagiolepis foreli Santschi
**Anoplolepis longipes* (Jerd.)
Paratrechina bourbonica (Forel)
**Paratrechina longicornis* (Latr.)
Paratrechina manni Donisthorpe
**Paratrechina minutula* (Forel) ssp. *atoma* Forel
Paratrechina stigmatica (Mann)
**Paratrechina vaga* Forel
**Paratrechina vividula* (Nyl.)
Paratrechina sp.
**Oecophylla smaragdina* (F.)
Opisthopsis manni Wheeler
Camponotus (*Colobopsis*) sp.
Camponotus (*Tanaemyrmex*) *irritans* (F.Sm.) var. *samoaensis* Santschi
**Camponotus* (*Myrmamblys*) *reticulatus* Roger var. *bedoti* Emery
Camponotus (*Myrmegonia*) sp.
Polyrhachis (*Hedomyrma*) *annae* Mann
Polyrhachis (*Myrmatopa*) *?osae* Mann
Polyrhachis (*Charyomyrma*) *rere* Mann
Polyrhachis (*Cyrtomyrma*) *rastellata* (Latr.) var. *fulakora* Mann
**Polyrhachis* (*Myrma*) *salomo* Forel.

© Commonwealth Agricultural Bureaux, 1959.



G. 1. Nutlets showing *Amblypelta* scars; in the ght-hand specimen the perianth scales have been moved.



FIG. 3. Mature nuts showing different degrees of damage by *Amblypelta;* from left to right, class 2,3,4 and 5.



IG. 2. Mature coconuts with scars; the right-and nut has scars caused by *Amblypelta;* the left-and one has been scarred by rubbing against its eighbours in a bunch.



FIG. 4. Nutfall observation plot M. I; Kukum, Guadalcanal.



FIG. 1. Crown of coconut palm with severe nutfall (crop "0").



FIG. 2. Crown of palm with moderate nutfall (crop "2"); note the scars on the nuts that remain.



FIG. 3. Crown of palm with normal crop, unaffected by nutfall (crop "3").



FIG. 4. Coconut spadix enclosed in muslim cage for observing the behaviour of ants in presence of *Amblypelta*. The crop is a full one, unaffected by nutfall (crop "4").

STUDIES ON THE COCONUT PEST, *PSEUDOTHERAPTUS WAYI* BROWN (COREIDAE), IN ZANZIBAR.

II.—SOME DATA ON THE YIELDS OF COCONUTS IN RELATION TO DAMAGE CAUSED BY THE INSECT.

By F. L. Vanderplank, Ph.D.

Entomologist, Coconut Pest Research Scheme, Zanzibar.

The coconut palm has never, as far as records go, given consistently good yields in East Africa, except in a few isolated places. Way (1953*a*) showed that the so-called "nutfall disease" there was due to necrotic lesions caused by nymphs and adults of a Coreid bug that is now known as *Pseudotheraptus wayi* Brown, and gave some assessments of crop loss, but there are no figures from which one can assess the overall loss for Zanzibar or elsewhere in East Africa.

Populations of *P. wayi* are affected to a considerable extent by the dominant ant populations. In Zanzibar there are three distinct ecological complexes:—

(a) The indigenous *Oecophylla-Pheidole* complex. *O. longinoda* (Latr.) is a tree-nesting species that is mainly predacious in habits, and strong colonies protect the palm against *Pseudotheraptus*. *Pheidole punctulata* Mayr, a ground-dwelling ant, exercises no control over *Pseudotheraptus*, but is antagonistic to *Oecophylla*. Under wet conditions, *Oecophylla* thrives, and under dry conditions, *Pheidole*. Other indigenous ants are present, but do not appear to have much influence on either of these two species of ants, or on the Coreid.

(b) The "crazy" ant, *Anoplolepis longipes* (Jerd.). This ant was imported into Zanzibar some 30–50 years ago and has spread over roughly 50–60 of the island's 640 sq. miles. It destroys *Oecophylla* and completely fails to control *Pseudotheraptus*.

(c) The "pugnacious" ant, *Anoplolepis custodiens* (F. Sm.), was accidentally introduced into Zanzibar about 1946. Mayr (1895) gives Zanzibar as a locality for this species, but at that time part of the mainland coast was included in the Zanzibar Protectorate. *A. custodiens* has spread within the area occupied by *A. longipes* since it was introduced (or re-introduced) in 1946 and occupies an area of about 10 sq. miles that was previously occupied by *A. longipes*. *A. custodiens* appears to exercise slight control over *P. wayi*, but it destroys *Oecophylla*.

The Department of Agriculture, Zanzibar, has kept detailed records of yields in its various plantations for a number of years and such records, together with surveys of the vidaka damage rate (hereafter referred to as V.D.R., defined (Vanderplank, 1958) as the percentage of the fallen fruiting bodies of the coconut palm, not exceeding three inches in length, that bear feeding scars of *P. wayi*) and the percentage of palms with colonies of *Oecophylla*, form a basis for assessing the extent of the loss caused by *P. wayi* in Zanzibar.

Description of Plantations.

The Department of Agriculture has, amongst others, the plantations that are grouped according to their location, and described, in Table I.

Up to 1946, the Marhubi plantation was dominated by *A. longipes*, but *A. custodiens* was introduced in 1946 and spread outwards. Steyn (1954) quotes Mayr (1895) as stating that *A. custodiens* had been found in Zanzibar. If *A.*

TABLE I.

Description of government plantations of coconuts in Zanzibar, 1955.

Group locality	Name of plantation	Approximate no. of palms	Soil type*	Ecological complex	Description of palms, and their height	Remarks
Chukwani (3–7 miles south (of Zanzibar Town)	Mazizini	5,012	Sandy *mchanga* over clay	*A. longipes*	Good, 40 to 65 ft.	Waterlogged in places during heavy rains
	Mbweni	10,000	Shallow *kinongo*; sandy *mchanga*	*A. longipes* (¾); *Oecophylla-Pheidole* (¼)	Poor to fair, 20 to 45 ft.	Suffers regularly from drought
	Mile 5	4,400	Shallow *kinongo*	*Oecophylla-Pheidole*	Fair to excellent, 35 to 50 ft.	Well drained
	Mile 6	2,500	Various: shallow *kinongo* with clay patches	,,	Poor to excellent, 20 to 90 ft.	Very mixed plantation
	Buyu	2,000	Shallow *kinongo –uwanda*	,,	Good, 30 to 90 ft.	
Mtoni (2–5 miles north of Zanzibar Town)	Marhubi**	6,000	Deep sandy *mchanga*	*A. custodiens*	Good to excellent, 40 to 70 ft.	Quarantine Station
	Mtoni**	9,000	Sandy *mchanga* over clay	*A. longipes* up to 1952, now replaced by *A. custodiens*	Good to excellent, 40 to 65 ft.	On gently sloping hillside
	Chumbuni	6,540	Red *mchanga*	*A. longipes*, except small portion	Fair to good, 30 to 50 ft.	Undulating, on crest of hillock; palms spaced 28 × 28 ft.
	Beit-el-Ras	2,600	*Kinongo*	*Oecophylla-Pheidole*	Fair, 40 to 60 ft.	Not so well drained as others in this group
	Kigomeni	3,940	Red *mchanga*	,,	Fair, 40 to 60 ft.	

Selem (about 11 miles north of Zanzibar Town)	Sakafuni	5,400	Red *mchanga*	*Oecophylla-Pheidole*	Fair	Apt to be waterlogged in heavy rains
	Mbuyuni	3,300	,,	,,	Fair	
Kidichi (10–14 miles NNE. of Zanzibar Town)	Langoni	5,200	Red *mchanga* on slopes, grey *mchanga* in valleys	*Oecophylla-Pheidole*	Good to excellent, 20 to 50 ft.	Apt to be waterlogged in parts in heavy rains
	Nguruweni	8,600	,,	,,	Good	,, ,, ,, ,,
	Kizimbani Kubwa	4,900	,,	,,	Good to excellent, 45 to 65 ft.	,, ,, ,, ,,
	Kizimbani Ndogo	3,700	,,	,,	Good, 50 to 70 ft.	,, ,, ,, ,,
	Kinuni Moshi	2,200	,,	,,	Good	,, ,, ,, ,,
	Kipange	1,400	,,	,,	Good to excellent	,, ,, ,, ,,
	Kidichi Mdo	8,000	,,	,,	Good to excellent, 40 to 70 ft.	,, ,, ,, ,,
	Kidichi Dole	4,000	,,	,,	Good to excellent	,, ,, ,, ,,
	Kidichi Bububu	4,000	Red *mchanga*	*A. longipes* (½); *Oecophylla-Pheidole* (½)	Fair to good	Planted closer and less regularly than other plantations

* For an explanation of the terms applied to these soil types, see Calton, Tidbury & Walker (1955).
** See notes in text on the changes in ant populations in these plantations.

custodiens was present then, it appears either to have died out or been present in such small numbers that it remained unnoticed up to 1946. By 1951, *A. custodiens* occupied the whole plantation; this was treated with a spray containing dieldrin in November and December 1953 and, as a result, the population of *A. custodiens* was reduced to a very low level, but some 18 months later it had regained its former density.

Similarly, in the Mtoni plantation, *A. longipes* was predominant up to 1952 but in that year *A. custodiens* started to invade the southern end of the plantation. This invasion was checked in 1953–54 by spraying with dieldrin, but *A. custodiens* has since advanced over the whole of the plantation, which is relatively free from woody weeds and has a scanty grass cover on which cattle graze.

Crop Records.

When the yields from all plantations are totalled there is not a very great annual variation, although yields from individual palms vary from nil to over 400 nuts per annum.

TABLE II.

Number of nuts gathered from the whole of Mazizini plantation from 1943 to 1955.

Year	No. of palms	Gatherings				Total	Mean nuts per palm
		1st	2nd	3rd	4th		
1943	5,800	12,310	12,372	12,010	6,034	42,726	7·4
1944	5,800	13,524	9,931	7,326	—	30,781	5·3
1945	5,800	7,928	7,234	8,014	—	23,176	4·0
1946	5,800	16,099	11,508	10,766	14,998	53,371	9·2
1947	5,800	12,634	2,094	5,232	7,398	27,358	4·7
1948	5,800	9,719	9,241	12,354	19,120	50,434	8·7
1949	5,800	19,241	11,835	8,955	15,357	55,388	9·6
1950	5,800	18,818	13,040	14,027	19,490	65,375	11·2
1951	5,700	8,846	7,523	11,030	13,082	40,481	7·1
*1952	5,600	25,746	17,552	16,780	9,856	69,934	12·5
*1953	5,400	8,410	2,572	—	21,950‡	32,932	6·1
*1954	5,200	18,461	9,990	7,552	10,213	46.216	8·9
*1955	5,012	24,427	25,004	17,977	20,013	87,421	17·5
Total	73,312	196,163	139,896	132,023†	135,561†	625,593	—
Average	5,640	15,090	10,761	11,002†	13,561†	48,123	8·5
Average per palm	—	2·7	1·9	1·9 (5)	2·4	8·5	—

It takes, on an average, 6,800 of these nuts to make one ton of copra.

* Includes experimental plots.

† The total and average for the 3rd picking are based on 12 years only, 1953 being omitted; similarly those for the 4th picking are based on 10 years only, 1944, 1955 and 1953 being omitted. The annual average thus does not tally with the sum of the quarterly averages.

‡ In 1953, the 3rd and 4th pickings were combined on account of a shortage of labour.

Coconuts are gathered by hand every three months in these plantations. Table II shows the variation in the yields obtained at Mazizini plantation from 1943 to 1955. From 1952, yields have been affected by experiments involving the application of insecticidal sprays in part of this plantation, and the number

of palms has dwindled as a result of land being taken over for building purposes. Since 1951, the V.D.R. has been regularly recorded from various parts of this plantation, and in the unsprayed areas the monthly mean value has varied between 60 and 80. *A. longipes* has been the dominant ant species at Mazizini since at least 1939. In 1948, only a few colonies of *Oecophylla* remained in a small pocket on the southern edge of the plantation, and it is these that Way (1953*b*) records as having been finally driven out in 1952. Since then, *Oecophylla* has re-established itself in the sprayed areas, but not in the unsprayed ones. The mean yield per palm over the whole area during 1943–1955 is 8·5 nuts (Table II). What should an area like this bear in the absence of *P. wayi*? Some indication can be obtained from the mean yield of palms in the sprayed area, which by 1955 had strongly established colonies of *Oecophylla*. These gave a mean yield of 78·8 nuts per palm in 1955, and even of these about 20 per cent. bore scars of feeding by *P. wayi*. Thus the average loss in this area due to *P. wayi* would appear to be about 70 nuts per palm per annum.

The yields from four plantations in the Chukwani group (Mbweni, Mile 5, Mile 6 and Buyu) over the period 1941–1955 are given in Table III. Of the four, Mbweni plantation, which is mostly infested by *A. longipes*, has given very poor yields, like Mazizini. A portion that was sprayed from March 1954 onwards yielded 46,028 nuts from 800 palms in 1955 (second gathering)–1956 (first gathering), or about 58 nuts per palm per annum, although *P. wayi* was only partially controlled. The rest of Mbweni gave 42,704 nuts over the same period, from 9,200 palms, or an average of 4·64 nuts per palm per annum. Here

TABLE III.

Annual yields from four plantations in the Chukwani group.
(Total nuts followed, in brackets, by nuts per palm.)

	No. of palms	Mbweni 10,000	Mile 5 4,400	Mile 6 2,500	Buyu 2,000
Year					
1941		82,020 (8·2)	88,526 (20·1)	76,286 (30·5)	41,688 (20·8)
1942		70,304 (7·0)	61,273 (13·9)	58,762 (23·5)	36,670 (18·3)
1943		87,313 (8·7)	95,168 (26·0)	65,589 (26·2)	44,514 (22·2)
1944		51,016 (5·1)	81,870 (18·6)	66,015 (26·4)	49,596 (24·8)
1945		54,293 (5·4)	66,501 (15·1)	41,853 (16·7)	45,313 (22·7)
1946		73,733 (7·4)	96,350 (21·9)	57,596 (23·0)	66,339 (33·2)
1947		56,817 (5·7)	63,392 (14·4)	26,460 (10·6)	35,230 (17·6)
1948		71,676 (7·2)	74,032 (16·8)	49,470 (19·8)	44,517 (22·2)
1949		78,121 (7·8)	86,967 (19·7)	57,880 (23·1)	46,254 (23·1)
1950		76,376 (7·6)	84,400 (19·2)	53,411 (21·4)	48,172 (24·1)
*1951		53,826 (5·4)	62,732 (14·3)	37,150 (14·9)	28,746 (14·4)
*1952		71,955 (7·2)	100,786 (22·9)	51,681 (20·7)	31,824 (15·9)
*1953		60,506 (6·1)	90,184 (20·5)	37,770 (15·1)	46,760 (23·4)
*1954		51,035 (5·1)	60,502 (13·7)	25,072 (10·0)	19,476 (9·8)
*1955		107,926 (10·8)	99,190 (22·7)	52,742 (21·1)	45,165 (22·6)

* Spraying experiments established in parts of Mbweni, Mile 5 and Mile 6 from the end of 1951 onwards.

again in the unsprayed area the V.D.R. was between 60 and 80 (average 72) throughout the year. There are a few colonies of *Oecophylla* in the southern end of this plantation, but many of the palms are in extremely poor condition.

The adjoining plantation on the south side, known as Mile 5 plantation, has an *Oecophylla-Pheidole* complex. Although the soil and conditions are very

similar to the Mbweni plantation, the yield is more than double that of the latter. In 1951, about 20 per cent. of the palms had colonies of *Oecophylla* and in 1955, 33 per cent. of the palms were so occupied, but even so the V.D.R. varied from 46 to 88 (average 60) during the latter year. It is to the presence of this population of *Oecophylla*, as well as to the superiority of the palms, that the relatively high yield is attributed.

Mile 6 plantation adjoins Mile 5 at the southern extremity of the latter and is very similar to it in many respects, although the soil is more variable. A survey here of 1,000 marked palms showed that 10 per cent. had colonies of *Oecophylla* in October 1952, and 39·4 per cent. in June 1955 after treatment with a selective insecticidal formulation (Vanderplank, 1958). Sixty palms that had strong *Oecophylla* colonies during 1953 yielded 3,924 nuts in 1954, or an average of 65·4 nuts per palm, which indicates what the area would bear were *P. wayi* controlled.

The Buyu plantation, to the south of Mile 6, is more isolated and is exposed to the prevailing south-east monsoon. Damage by *P. wayi* is less prevalent here than in the other plantations in this group, although only about the same percentage of the palms is colonised by *Oecophylla*, and the yields are correspondingly higher. The annual total yields from 1944 to 1955, inclusive, of all the Chukwani group of plantations are given in Table IV, and the largest deviation from the 12-year mean in any year (omitting 1955, when yields were probably influenced by the experimental spraying done in 1954) is 27·0 per cent., which is less than might be expected.

TABLE IV.

Variation of annual yields in the Chukwani group of plantations, 1944–1955.

Year	Total yield (nuts)	Deviation from 12-year mean	
		Nuts	%
1944 ..	279,278	— 6,435	— 2·2
1945 ..	231,136	— 54,577	— 19·1
1946 ..	347,389	+ 61,676	+ 21·6
1947 ..	209,257	— 76,456	— 26·7
1948 ..	290,129	+ 4,416	+ 1·5
1949 ..	324,610	+ 38,897	+ 13·6
1950 ..	327,734	+ 42,021	+ 14·7
*1951 ..	222,945	— 62,768	— 22·0
*1952 ..	327,185	+ 41,472	+ 14·5
*1953 ..	268,152	— 17,561	— 6·2
**1954 ..	208,300	— 77,413	— 27·0
**1955 ..	392,445	+ 106,732	+ 37·3
Total ..	3,428,560		

Mean yield (1944–1955, inclusive), 285,713 nuts per annum.

* Small-scale spraying experiments were carried out in the area this year, but these had no significant effect on the total yield of the area.

** Extensive spraying experiments were carried out in the area this year.

In the Mtoni group of plantations, very similar results have been obtained (Table V). Amongst this group is the Marhubi plantation where, up to 1947, when the dominant ant was *A. longipes*, average yields were between 20 and 40 nuts per palm per annum. From 1947 onwards, as *A. custodiens* replaced *A. longipes*, yields averaged from 22 to 46 nuts per palm per annum. There was a noticeable fall in yield in 1951, following an attempt to eradicate *A. custodiens*, and again in 1954, following a further attempt to control this

undesirable ant; in these years, the yield fell to 21 and 22 nuts per palm per annum, respectively. From this it would appear that *A. custodiens* exercises some control of *P. wayi*. I have observed *A. custodiens* carrying off 2nd- and 3rd-instar nymphs of *P. wayi* on several occasions. The V.D.R. was high in January, February and early March 1955 (60 to 70), and during the rains in the

TABLE V.

Total annual yield of the Mtoni group of plantations. The deviations from the 12-year mean are compared with those of the Chukwani group (from Table IV).

Year	Total yield (nuts)	Deviation from mean		% deviation, Chukwani group
		Nuts	% of mean	
1944	700,018	+ 187,686	+ 36·7	— 2·2
1945	468,506	— 43,826	— 8·6	— 19·1
1946	629,552	+ 117,220	+ 22·8	+ 21·6
1947	362,508	— 149,824	— 29·1	— 26·7
1948	479,440	— 32,892	— 6·4	+ 1·5
1949	653,735	+ 141,403	+ 27·5	+ 13·6
1950	546,655	+ 34,323	+ 6·7	+ 14·7
1951	363,842	— 148,490	— 28·9	— 22·0
1952	608,990	+ 96,658	+ 18·9	+ 14·5
1953	465,857	— 46,475	— 9·1	— 6·2
1954	361,908	— 150,424	— 29·3	— 27·0
1955	506,977	— 5,355	— 1·1	+ 37·3
Total ..	6,147,988			

Mean yield (1944–1955, inclusive), 512,332 nuts per annum.

latter part of March and April it fell below 40. In May, it averaged just under 50, and from then to January 1956 it varied between 65 and 80. The rains in November and December were light. Observations in the field suggested that, during the heavier rains, many mealybugs tended by *A. custodiens* died from fungal infection and that *A. custodiens* was forced to rely more upon other insects as food. After the heavy rains had finished, *A. custodiens* once again obtained most of its food from various species of mealybug (see Steyn, 1954). Since *A. custodiens* destroys *Oecophylla*, and heavy rain in Zanzibar is restricted to a few months only, it would appear that *A. custodiens* will not be much more desirable than *A. longipes*, which it is rapidly replacing, and which has a very adverse affect on coconut yields.

Mtoni plantation is very similar to Mazizini except that instead of being flat it is on undulating ground; its yields are about the same as those of Mazizini. A third plantation of this group, Chumbuni, is very similar to the Mbweni plantation. Both are heavily infested with *A. longipes* and have only fair to good palms; in both cases, the yield over the past 15 years has been only from 4 to 10 nuts per palm per annum. The main difference is that Chumbuni is on deep red sandy soil whilst Mbweni is on shallow sandy soil over coral.

Two further plantations of the Mtoni group, Kigomeni and Beit-el-Ras, carry similar palms, with much the same ecology and yields as the Mile 5 and Buyu plantations in the Chukwani group, but the soils differ.

The annual yield of nuts from the Mtoni group of plantations, and the deviations of this from the 12-year mean (1944–1955) compared with those of the Chukwani group, are shown in Table V. Except in 1944, when there was a difference of over 34 between the two percentage deviations, and in 1955, when

the difference exceeded 38 but was due probably to the insecticidal sprays used on part of the Chukwani group, the percentage deviations of the two groups in any given year do not differ greatly from each other. This might be expected, as they are similar groups of plantations and only six miles apart.

TABLE VI.

Total annual yield of the Kidichi group of plantations.

Year	Total yield (nuts)	Mean nuts per palm	Deviation from mean	
			Nuts	% of mean
1944	1,060,369	25·2	— 158,949	— 13·0
1945	1,277,091	30·4	+ 57,773	+ 4·7
1946	1,339,917	31·9	+ 120,599	+ 9·9
1947	1,229,497	29·3	+ 10,179	— 0·8
1948	1,025,673	24·3	— 193,645	— 15·8
1949	1,528,626	36·5	+ 309,308	+ 25·3
1950	1,467,232	35·0	+ 247,914	+ 20·3
1951	926,219	22·1	— 293,099	— 24·0
1952	1,262,651	30·0	+ 43,333	+ 3·5
1953	1,177,056	28·1	— 42,262	— 3·5
1954	1,063,418	25·3	— 155,900	— 12·8
1955	1,274,069	30·4	+ 54,751	+ 4·5
Total ..	14,631,818			

Approximate number of palms, 42,000. Mean yield (1944–1955, inclusive), 1,219,318 nuts per annum (29·0 nuts per palm).

The Kidichi group of plantations are all on better soils than those of the plantations discussed above. These are mostly deep, red soils, and all the group, except part of Kidichi Bububu, have the *Occophylla-Pheidole* ant complex. Table VI gives the annual total yields for the whole group, with the means per palm and deviations from the 12-year mean. Here again, the maximum deviation from the 12-year mean is not large, being only 25·3 per cent.

No records of the V.D.R. on the Kidichi plantations were kept for any of the periods covered by Table VI. The V.D.R., however, was recorded on six 20-acre plots, each containing about 1,000 palms, within this group of plantations during 1955–56. No insecticides were applied to these areas during 1955 and only one small plot of 100 palms had been used previously for such a purpose. Records from these six plots were obtained by collecting as many as possible of the fallen vidaka twice each week and examining them, and the weekly trials have been combined to form Table VII.

It will be seen from Table VII that the V.D.R. varied between 41·5 and 55·5, with a mean value of 47·7 over the whole 12 months of observations. The crop of mature nuts corresponding to these figures for V.D.R. was gathered in the second, third and fourth harvestings of 1956 and the first of 1957. The plots themselves were not harvested separately, but the total from the whole of the Kidichi plantations (except Kidichi Bububu, in which there was no record plot) was 1,104,160 nuts from 38,000 palms, an average of 29·05 nuts per palm per annum. This is almost the same as the 12-year average from the whole group (see Table VI).

Sufficient data are not yet available to correlate V.D.R. (X) and yield (Y) in the Kidichi area, although they are for certain plots at Mazizini and Chukwani (Vanderplank, 1958), which have a lower rainfall and less fertile soils. The

TABLE VII.

Monthly values of the vidaka damage rate (V.D.R.) from 6 plots (20 acres each) in the Kidichi group of plantations, 1955–1956.

Month	No. of vidaka collected	No. of vidaka showing lesions caused by *P. wayi*	% with lesions (V.D.R.)
1955			
May	7,799	3,327	42·7
June	7,520	3,136	41·6
July	6,528	3,887	44·4
August	5,743	2,607	45·4
September	5,817	2,852	49·2
October	5,990	2,844	47·5
November	6,117	3,388	55·5
December	6,018	3,282	54·5
1956			
January	6,343	3,184	50·3
February	7,167	3,133	43·6
March	5,213	2,417	46·5
April	9,025	3,750	41·5
Total	79,280	37,807	47·7

regression for what is potentially the best of these plots, Mazizini B, is Y = 19·8 − 0·287 X, and here a value of X = 47·7 would correspond with a yield of Y = 6·1 nuts per quarter, or 24·4 per annum. This is 4·65 nuts per annum less than that obtained at Kidichi (see above), a result that might be expected in view of the more fertile conditions at Kidichi. If *P. wayi* were eradicated at Mazizini B, a maximum yield of 19·8 nuts per palm per gathering, or 79·2 per

TABLE VIII.

Yield of coconuts from all Government plantations, 1944–55.

Year	Total nuts from all plantations	Average nuts per palm	Variation from 12-year mean	
			Nuts	% of mean
1944	2,401,126	23·4	+ 95,277	+ 4·1
1945	2,241,481	21·9	− 64,368	− 2·8
1946	2,668,003	26·0	+ 362,154	+ 15·7
1947	2,064,879	20·1	− 240,990	− 10·4
1948	2,046,330	20·0	− 259,519	− 11·2
1949	2,865,032	27·9	+ 559,183	+ 24·3
1950	2,647,140	25·8	+ 341,291	+ 14·8
1951	1,709,130	16·7	− 596,719	− 25·8
1952	2,451,625	23·9	+ 145,776	+ 6·3
1953	2,201,673	21·5	− 104,176	− 4·5
1954	1,966,620	19·2	− 339,232	− 14·7
1955	2,407,152	23·5	+ 101,303	+ 4·4
Total ..	27,670,191	—	—	—
Mean ..	2,305,849	22·5	—	—

Total palms, 102,692.

TABLE IX.

Yields from palms protected by *Oecophylla* compared with those from the whole plantation (all data from unsprayed areas).

Year	Plantation	Acreage	With *Oecophylla* colonies nesting in the palms			Plantation as a whole including those palms with *Oecophylla*		
			No. of palms	Total yield	Average per palm	No. of palms	Total yield	Average per palm
1953	Mile 6	50	181	13,163	72·7	2,500	37,770	15·1
1954	Mbweni	160	450	18,193	40·3	8,000**	51,035	6·4
1956/57	Kidichi Dole (upper control plot)	20	72	8,191	113·8	1,011	50,262	49·6
*1956/57	Kidichi (experimental plot)	100	183	13,567	74·2	4,750	157,555	33·2
*1956/57	Kidichi Dole (lower control plot)	50	99	7,183	72·0	2,042	75,570	37·0
	Total	380	985	60,297	61·2	18,303	372,192	20·3

* Three pickings only; prior to effect of spraying experiments.
** Palm yields not recorded individually.

annum, would be expected, from extrapolation of the regression. Kidichi and most of the other coconut-producing areas of Zanzibar might be expected to have higher potential yields than Mazizini B, and I estimate it at an average of 90 nuts per palm per annum. Since the actual yield is only about 29 nuts, this would mean that some two-thirds of the potential crop is being lost in the best coconut areas of Zanzibar.

When all the Government plantations are considered together for the 12-year period 1944–1955 (Table VIII), the variation from year to year is less than in the individual plantation groups, being only about ±25 per cent. of the 12-year mean, which is 22·5 nuts per palm. Williams (1949) states that, in 1944, yields of coconuts taken on four Government plantations averaged 40, 43, 56 and 76 nuts per palm. These figures were taken from the annual reports of the Department of Agriculture and were based on averages from the palms from which nuts were gathered, and not on the total number of palms (of bearing age) in the plantations.

Although the Government plantations show a fairly steady annual yield, the export figures indicate larger variations. This is because many more variables are involved. Coconuts are exported in the form of nuts, copra, coconut oil and coconut cake, and all these are also used locally to an unknown extent. More coconuts are consumed locally when the clove crop is large.

Estimation of the Financial Loss caused by *P. wayi*.

It is not possible to say exactly what loss *P. wayi* causes to the coconut industry in Zanzibar, but there are at least two sound methods of estimating it. The first method is to calculate the average value of the V.D.R. for the main coconut-growing areas of Zanzibar, and use this to estimate the equivalent loss in mature nuts. The mean value of the V.D.R. was calculated from 200 samples, each of 500 fallen vidaka, collected in June–August 1953 from 200 sites arranged to cover the whole of the main coconut-growing areas in Zanzibar, and the figure obtained was 60·6. As will be seen from Table VII, there was a 14 per cent. variation during the year 1955–56 for the Kidichi group of plantations, so that although the overall data for Zanzibar were collected during June, July and August, when the damage rate is near its minimum, it might be safer to take a value of 50 as a conservative estimate of the V.D.R. for the whole island. It has been shown in the first of this series of papers (Vanderplank, 1958) that V.D.R. (X) and yield (Y) are related by the regression, $Y = a + bX$, and hence if $X = 50$, the loss in yield, expressed as a percentage of the potential yield, a (that obtained when $X = 0$), can be shown to be $5{,}000\ b/a$. The values of a and b have been determined for five experimental plots in Zanzibar (*op. cit.*, Table XI) and their means are 16·4 and −0·222, respectively. The loss of crop associated with a V.D.R. of 50 is thus 67·5 per cent. of the potential crop; in other words, twice as much is being lost as is obtained. There is no reason to suppose that with increased crops any more nuts would be consumed locally, so that any increase of yield would be exported.

It should be noted that control of *P. wayi* not only increases the numbers of nuts matured, but considerably increases their average copra content. Way (1953*a*) gives figures to show that there was 47 per cent. more copra from undamaged nuts than from those badly damaged by *P. wayi*. In 1954, a heap of nuts from an unsprayed area was divided into those free from damage (about 1,000 nuts) and those damaged by *P. wayi* (about 2,000 nuts). These were all converted into copra, when it was found that there was 20 per cent. more copra per nut in the undamaged as compared with the damaged nuts.

The second method of calculating the loss of crop caused by *P. wayi* is to compare the yields of palms exposed to attack by *P. wayi* with those of palms protected by *Oecophylla*. Records have been kept over five years (1951–56) of

TABLE X.

Quantity and value of exports of coconuts and coconut products, Zanzibar, 1949–56.

Year	Copra		Coconut oil		Coconuts		Total value (£)
	Tons	Value (£)	Cwt.	Value (£)	Cwt.	Value (£)	
1949 ..	7,922	424,938	130,791	582,039	1,174	1,217	1,008,194
1950 ..	—	—	160,179	789,086	2,182	907	786,993
1951 ..	25	1,931	101,963	633,866	270	457	636,254
1952 ..	2,558	146,334	105,252	479,477	13,506	11,652	637,463
1953 ..	5,815	403,721	94,317	465,990	17,695	29,826	899,537
1954 ..	5,805	404,735	79,540	410,251	19,039	26,759	841,745
1955 ..	5,446	325,215	74,204	333,692	22,971	35,165	694,072
1956 ..	6,590	382,312	72,337	327,802	18,889	28,962	739,076
Total ..	34,161	2,089,186	818,583	4,019,203	95,726	134,945	6,243,334
Average	4,270	261,148	102,323	502,400	11,966	16,868	780,417

yields from 4,000 individual palms in the Chukwani group of plantations and more recently from 9,000 palms in the Kidichi group. Some of these palms have been used for insecticidal experiments, but Table IX gives the yields from the control (unsprayed) areas of the plantations, and also from those palms in which strong colonies of *Oecophylla* (which are distributed at random) were recorded for the year prior to and during that in which the yield was recorded. From this Table it will be noted that on the poorer soils (Mbweni and Mile 6) the mean yield of palms inhabited by *Oecophylla* is several times that of the whole unsprayed area of the plantation, which includes both these palms and others where *Oecophylla* has only been recorded occasionally. *Oecophylla* does not necessarily stay permanently in any one palm and frequently the whole colony will move to another one. In the case of the plantations on better soils (Kidichi Dole and Kidichi), data are available at the time of writing for three gatherings only out of the four per annum, but this should not affect the proportional increase due to the protection afforded by *Oecophylla*; in these plantations, the yield from palms protected by *Oecophylla* is just over twice that of the plantation as a whole.

Two methods have been given, above, of estimating the loss of crop caused by *P. wayi*. The first, in which the potential crop is estimated by extrapolating the regression of yield on vidaka damage rate to the point where the latter is nil, is theoretical and such yields may not be reached in practice; it gives the higher limits of damage and suggests that 67·5 per cent. of the potential crop is lost, or that, under present conditions, twice as much is lost as is harvested. The second method, being based on the measurement of the yields of *Oecophylla*-protected palms, suffers from the disadvantage that *Oecophylla* does not give complete protection from *P. wayi* and may itself reduce the crop by preventing insect pollination; it suggests that half the potential crop is lost to *P. wayi* in the best coconut-growing areas and a considerably higher proportion in other areas, so that at least as much is lost as is harvested.

The amount of crop lost, in terms of present production, being known (within, admittedly, wide limits), this can now be converted into terms of cash. One method is to ignore local consumption and to use, as an estimate of production, the value of the coconuts, copra and oil exported, thus underestimating the true financial loss; this value has varied from £636.254 to £1,008,194 per annum during 1949–1956 (Table X). A second method involves estimating the present production of nuts and using the price of unhusked nuts to get an estimate of total value. This method depends on knowing the number of bearing palms in Zanzibar and the present average yield. Now the whole of Zanzibar was covered by aerial photographs in 1947. Using these in conjunction with a large-scale map, I calculated the present area under coconuts (excluding the very numerous odd palms and small isolated plots) to be about 104,000 acres. The density of the palms varies very considerably but, on an average, 50 ± 10 per acre would be a fair estimate, giving 5,200,000 palms. The overall 12-year average yield from the Government plantations is 22·5 nuts per palm per annum (Table VIII), and if these are considered a fair sample of the island's plantations the present yield for the whole island is about 117 million nuts per annum. The value of these nuts varies with world market prices, and it is increased if they are manufactured into copra, or coconut oil and cake. However, the proportions so processed likewise vary with world demands, so that the total crop can best be valued as unhusked nuts. The prices offered for unhusked nuts in Zanzibar from 1948 to 1956 is given in Table XI; it has varied from Shgs. (E.A.) 90–150 per thousand. This gives a minimum value for the crop of £526,500 and a maximum of £877,500 per annum, based on a yield of 117 million nuts.

Taking, therefore, the loss caused by *P. wayi* as being at least equal to and possibly twice the size of the crop produced under present conditions, and taking

the value of that crop as £636,254–£1,008,194, if based on values of exports, or £526,500–£877,500, if based on values of unhusked nuts, it appears that the minimum and maximum estimates of the financial loss caused annually by *P. wayi* are of the order of £500,000 and £2 million, respectively.

TABLE XI.

Coconut prices in Zanzibar, 1948–56 (prices in shillings (E.A.) per thousand nuts).

Year	Minimum	Maximum	Yearly average
1948 ..	70	110	90
1949 ..	100	125	110
1950 ..	100	160	125
1951 ..	140	185	150
1952 ..	55	150	125
1953 ..	80	170	120
1954 ..	90	170	115
1955 ..	75	140	105
1956 ..	90	145	115

Summary.

In the second of this series of papers on the losses caused by the Coreid, *Pseudotheraptus wayi* Brown, to coconuts in Zanzibar, descriptions are given in summary form of a number of Government-owned plantations of coconuts on the island, together with the yields recorded over the 12 years, 1944–55. The variation from year to year in any group of plantations is not large, and over all those considered does not exceed 25·8 per cent. of the 12-year mean.

In the plantations on poorer soils, predominantly occupied by the ants *Anoplolepis longipes* (Jerd.) or *A. custodiens* (F. Sm.), the vidaka damage rate (V.D.R.) during 1955 varied from 60–80. The plantations on better soils are occupied predominantly by a complex of *Oecophylla longinoda* (Latr.) and *Pheidole punctulata* Mayr and the V.D.R. determined on a part of these in 1955–56 varied from approximately 41 to 55, with a mean of 47·1. The mean value of the V.D.R. calculated from 200 localities taken at random in Zanzibar during June–August 1955 was 60·6. Taking a value of 50 as a conservative estimate of the V.D.R. for the whole island, and inserting this in the regression equation $Y = a + bX$ relating yield (Y) with V.D.R. (X), derived in the first of this series of papers, together with the average values of the constants a and b obtained therein, it is shown that about two-thirds of the potential crop of coconuts is lost as a result of damage by *P. wayi*.

Comparison of the yields from palms occupied by *Oecophylla* in two of the plantations on better soil with those of the whole of those plantations suggests that about one-half of the potential crop is being lost.

The annual value of the total exports of unconverted nuts and coconut products (copra and coconut oil) varied from £636,254 to £1,008,194 during 1949–56, and the annual value of the total production of nuts, calculated from the estimated total acreage (104,000), the number of palms per acre (50), the 12-year average yield per palm on Government-owned plantations (22·5 nuts per annum) and the market price in 1948–56 (Shgs. (E.A.) 90–150 per thousand nuts), is £526,500 to £877,500. Taking into consideration the lower and upper estimates of the amount of crop lost and of the value of what remains, the minimum and maximum estimates of the financial loss caused by *P. wayi* in Zanzibar are of the order of £500,000 and £2 million, respectively.

Acknowledgements.

The figures of yield in this paper are from the Department of Agriculture's official figures and due acknowledgements are made to Mr. A. K. Briant, O.B.E., Director of Agriculture, under whom this work was carried out. The author also wishes to thank Mr. G. E. Tidbury, Senior Agricultural Officer, and the Manager of Plantations, formerly Mr. I. G. C. Squire and later Mr. Ali Khamis, for access to the figures and their helpful co-operation; also Mr. P. B. Sweeney, Acting Comptroller of Customs, Mr. J. G. D. Kerr and the Clove Growers Association for their help on coconut export figures and average market prices.

References.

Calton, W. E., Tidbury, G. E. & Walker, G. F. (1955). A study of the more important soils of Zanzibar Protectorate.—*E. Afr. agric. J.* **21** pp. 53–60.

Mayr, G. (1895). Afrikanische Formiciden.—*Ann. naturh. Hofmus. Wien* **10** pp. 124–154.

Steyn, J. J. (1954). The pugnacious ant (*Anoplolepis custodiens* Smith) and its relation to the control of *Citrus* scales at Letaba.—*Mem. ent. Soc. S. Afr.* no. 3, 96 pp.

Vanderplank, F. L. (1958) Studies on the coconut pest, *Pseudotheraptus wayi* Brown (Coreidae), in Zanzibar. I. A method of assessing the damage caused by the insect.—*Bull. ent. Res.* **49** pp. 559–584.

Way, M. J. (1953*a*). Studies on *Theraptus* sp. (Coreidae); the cause of the gumming disease of coconuts in East Africa.—*Bull. ent. Res.* **44** pp. 657–667.

Way, M. J. (1953*b*). The relationship between certain ant species with particular reference to biological control of the Coreid, *Theraptus* sp.—*Bull. ent. Res.* **44** pp. 669–691.

Williams, R. O. (1949). The useful and ornamental plants in Zanzibar and Pemba.—497 pp. Zanzibar Govt. & London, Crown Agents.

© Commonwealth Agricultural Bureaux, 1959.

STUDIES ON THE COCONUT PEST, *PSEUDOTHERAPTUS WAYI* BROWN (COREIDAE), IN ZANZIBAR.

III.—A SELECTIVE RESIDUAL INSECTICIDAL FORMULATION AND ITS EFFECTS ON THE ECOLOGY OF THE INSECT.

By F. L. Vanderplank, Ph.D.

Entomologist, Coconut Pest Research Scheme, Zanzibar.

The Coreid, *Pseudotheraptus wayi* Brown, causes heavy losses to the coconut crop in East Africa, the loss in Zanzibar alone being estimated at between £500,000 and £2 million per annum (Vanderplank, 1959). It is controlled to a limited extent in nature by various predators, of which the red tree ant, *Oecophylla longinoda* (Latr.), is by far the most important (Way, 1951, 1953). Way (1953) demonstrated that *P. wayi* could be controlled by an insecticidal dust containing 0·4 per cent. γ BHC (lindane) but that, in palms so treated, ants such as *Oecophylla* were eradicated and the palms became smothered with Coccids, notably the Diaspidid, *Hemiberlesia lataniae* (Sign.).

An insecticidal formulation was therefore sought that would kill *P. wayi* and persist on coconut palms for at least 2–3 weeks. It was desirable that the formulation should also kill secondary pests but not bees nor the beneficial ant, *O. longinoda*.

During the course of numerous laboratory and field experiments, formulations containing DDT and various synthetic resins were tested; the original reason for the inclusion of resin was to prevent the DDT from being absorbed by the parts of the coconut palm on which it was deposited.

Development of the Formulation.

A large selection of synthetic resins was obtained from various manufacturers, and their solubility in mineral and coconut oils was noted. Those resins which were found sufficiently soluble in mineral oils but not in coconut oil were formulated with various proportions of DDT and the crystal form of the residues and toxicity of the latter to nymphs of *P. wayi* were noted. This work was considerably aided by the appearance at that time of a paper on the subject by van Tiel (1952) although that author does not specify the resin he used. As a result of numerous experiments in Zanzibar, a proprietary coumarone indene resin * was found that was soluble in mineral oils but not in coconut oil, and that improved the residual toxicity to certain groups of insects of the DDT with which it was formulated. It was found that the proportion of one part resin to ten parts DDT gave optimal effect, in terms of the kill of nymphs of *P. wayi* allowed to walk on a treated surface for one minute. This result is in line with van Tiel's conclusions.

The first experiments with " 10 DRDK " (see p. 153) involved its application to 610 palms, at first every three months and later bimonthly, over a period of three years. They were carried out with pneumatic hand-sprayers giving droplets with diameters ranging from 100 μ to over 800 μ. Ladders were used to reach

* " Epok " coumarone indene resin.

the crowns of the palms, and only the centre of each crown with its inflorescences and bunches of nuts was sprayed. Detailed notes of the ant populations of the palm crowns were kept. Within a few months certain changes were noted, the most important of these being that palms with *Occophylla* nesting in them retained this ant in increased numbers, but that where small species of ants (such as *Pheidole* spp., *Crematogaster* spp. and *Paratrechina longicornis* (Latr.)) or *Anoplolepis longipes* (Jerd.) were either nesting or foraging in the crown, they had been eradicated. No change was noted in regard to other, larger, species of ants, such as *Polyrhachis* spp. and various indigenous species of *Camponotus*. Laboratory tests showed that the solution was equally lethal to all species tested when applied as an aerosol, but that the residual deposits were lethal only to smaller species of ants, with the single exception of *A. longipes*, which is about the same size as the smaller individuals of *O. longinoda*.

Potts & Vanderplank (1945) suggested that the pulvilli might be a deciding factor in the effectiveness of DDT residues against various species of insects and that the smaller the crystal size the more lethal the residue. Lewis (1954) claims that the pulvilli are unimportant in this respect, and in fact none of these species of ants has pulvilli. When various species of ants were observed under a lens in process of crossing various surfaces treated so as to afford a type of DDT residue in which the DDT crystals are vertical to the surfaces, it was noticed that the bodies of the smaller species rubbed against the apices of the clumps of crystals, but the bodies of the larger species were held clear. In the apparently anomalous case of *A. longipes*, a large species that is affected as though it were a small one, observations revealed a possible explanation, namely, that whereas other species hold their bodies well away from the surface on which they are walking, the body of *A. longipes* is carried near the surface, despite the comparatively long legs, and so the body comes in contact with the DDT crystals. If this theory is correct, then if the size of the crystals is increased, the DDT should become lethal to the larger species. When this was tested it was found that larger DDT crystals are indeed lethal to the larger as well as the smaller species of ants. This explains why the usual straight solutions of DDT in mineral oil were ineffective against any of the 30 species of ants tested in Zanzibar. When DDT, dissolved in kerosene or similar mineral oil is allowed to evaporate on glass or other surfaces, it forms flat rhombic and needle-like crystals lying parallel to the surface. DDT can also be formulated by dissolving 7 parts 80 per cent. p,p′DDT and 0·7 part cetyl alcohol in 100 parts highly refined kerosene (all parts by weight), so that it gives rise to 2–3 mm. residual crystals, lying parallel to the surface. This type of surface was not found to be very lethal towards the larger species of ants.

Although lindane and dieldrin can be affected as regards their persistence and the nature of their crystal residues by the addition of resins and other substances, no selective action has been found with either of these insecticides. After the selective action of DDT in different crystal forms had been noticed, an extensive investigation was undertaken into the factors affecting the formation and size of crystals, and their residual properties and selectivity, both in laboratory and large-scale, field experiments.

Factors affecting the Formulation of Crystal Residues.

Van Tiel (1955) gives an account of his own and others' work on the influence of resins on crystal size and toxicity of insecticidal residues. In my own work, most of which was carried out before van Tiel's account was published, I obtained similar results and came to the same conclusions. Many authors quoted by him found, as did Potts & Vanderplank (1945) and Vanderplank (1947), that the smaller the DDT crystals the higher the insect mortality, but Parkin & Green

(1945, 1947) and Van den Brande, Van den Hende & Jacobs (1951) came to the opposite conclusion.

The rate of evaporation of the solvent is one major factor affecting crystallisation of the residues. This will depend on temperature, barometric pressure and air movement, but within certain limits, such as those ruling in Zanzibar (temperature range 70°–90°F., barometric pressure 29·5 to 30·0 mm. Hg, relative humidity 50 to 100 per cent.), the evaporation rate does not affect the size of the crystals formed from DDT–resin, DDT–paraffin wax or DDT–cetyl alcohol formulations, although it does so in the case of DDT–mineral oil formulations. This is because the resin, paraffin wax or cetyl alcohol slows up the final evaporation of the solvent and releases it only slowly; these substances also act as solid solvents of DDT.

A large number of resins, of various grades, with and without the addition of plasticisers, were tested in the laboratory for their effect on crystalline residual deposits of DDT. Since other workers are investigating this type of problem in detail, the full results of these experiments are omitted, except those in respect of the formulations that have been used for extensive experiments.

The most useful formulation, as far as the *Pseudotheraptus* problem was concerned, was obtained by dissolving 235 lb. 80 per cent. p,p′DDT with 23·5 lb. of the proprietary resin * dissolved in 100 gal. diesoline and 100 gal. power kerosene. The mixture of power kerosene and diesoline is heated to between 40 and 45°C., and the crushed resin added. When this is dissolved, the DDT is added and dissolved, and the solution is finally filtered. This solution contains just over 10 per cent. p,p′DDT by weight and is known by the abbreviation 10 DRDK. Under the tropical conditions in which it has been used, this gives a residue of groups of needle-like crystals, projecting either vertically or at an angle to the sprayed surface, and between 10 and 120 μ long and 2 to 10 μ in both width and breadth. The properties of this formulation are described later.

Residues consisting of large crystals can be obtained in several ways, such as using all diesoline oil instead of a mixture of diesoline and kerosene. The addition of a heavy mineral oil to the diesoline, or the addition of a plasticiser, such as dimethyl phthalate, has the same effect. Crystal shape and size also vary with the type of resin used. Large crystals, 2–3 mm. long and lying horizontally along the sprayed surface, can be obtained from 0·7 per cent. cetyl alcohol in kerosene.

Residues consisting of smaller crystals can be obtained by using more volatile solvents, such as highly refined kerosene, xylene, benzene, or acetone, by using harder grades of resin, or by increasing the proportion of resin to DDT. When the coumarone indene resin is more than 20 per cent. of the DDT content, it retains all the DDT and no DDT crystals are obtained.

Droplet size appears to have little effect on ultimate crystal form. A 100-μ droplet of 10 DRDK will form a bunch of needle-like crystals, whereas one of 50 μ will form two or three crystals of the same size. Small droplets, however, limit the size of crystals formed with the formulations giving larger crystals.

Properties of 10 DRDK Formulation.

Since the 10 DRDK formulation is a super-saturated solution it may start to crystallise if its temperature falls below 70°F., but this is not likely to happen in Zanzibar. Droplets 80–160 μ in diameter exposed on a glass plate in an air stream of 5–7 m.p.h. at 85°F. took 2½ hours for the solvent to evaporate sufficiently for the residue to solidify. The loss of solvent from droplets falling through the air was tested by suspending magnesium-oxide plates inside a well and allowing the

* Epok coumarone indene resin, grade C.469.

droplets to fall down the shaft on to them. Table I gives the data obtained in a series of such experiments; the loss was high initially, but decreased with the distance fallen.

When the formulation is allowed to dry on a clean sheet of glass or smooth paper, or a similar surface, it gives rise to a super-saturated gummy residue, which can remain unchanged for a period of 2–3 weeks without crystallising,

TABLE I.

Decrease in size of droplets while falling.

Distance below nozzle (ft.)	Mean droplet diameter in microns (average of sample of 500 droplets)	% decrease in droplet diameter per foot fallen in successive intervals
3	110	—
6	102	2·7
9	98	1·3
15	90	1·3
20	87	0·6
35	85	0·1
Total loss (3–35 ft.)		7·1

provided that the droplets are not mechanically disturbed. This agrees with the findings of Parkin & Green (1945, 1947). An insect walking across such a super-saturated film causes the DDT to crystallise out wherever the film is touched, giving a visible record of the insect's tracks, which is characteristic of the species. Normally, crystallisation is promoted by foreign particles present in the formulation, on the sprayed surface, or in the atmosphere as well as by contact with insects. It requires 24–48 hours at the temperatures prevailing in Zanzibar for any crystals to be produced and the process continues for several days or even weeks. These crystals have the appearance of "branched" bunches, due to smaller crystals lying at an angle across the larger ones. The size of the crystals varies from 10 × 2 × 2 μ to 120 × 10 × 10 μ, the commonest size being about 40 × 5 × 5 μ. The clumps of crystals stand out as much as 1·5 mm. from the surface. It is these clumps of crystals that are selective in action by reason of their size, the solution itself being lethal to all the species of insects tested to date.

Persistence of Residual Crystals.

The persistence of the residual crystals is affected by: (a) initial dosage, (b) material to which the formulation is applied, (c) exposure to sunlight, rain, etc.

The loss of DDT and its effectiveness on various small species of ants was tested by dipping one-inch-wide strips of good quality, smooth-surfaced, brown paper in 10 DRDK, allowing excess liquid to run off, and attaching one of these around the trunks of each of 100 coconut palms in the field. Another 30 strips were hung up in the laboratory. Dr. J. T. Martin, of the Horticultural Research Station, Long Ashton, England, undertook to analyse the DDT content of sample strips sent to him at regular intervals. The strips tested in the field had been pinned around coconut palms that had either *Pheidole* sp. or *Anoplolepis longipes*, together with other species of ants, foraging on them. A column of ants was continually moving up and down, some 30–300 passing each point per minute. *A. longipes* was most active during the daytime, *Pheidole* sp. at night. The paper

TABLE II.

DDT content of paper bands treated with 10 DRDK and exposed in the field.
(Analysis carried out by Dr. J. T. Martin.)

Date	Approx. no. weeks exposed	Band no.	Mean content (μg. total DDT per sq. cm.)
12.iv.54 ..	0	125	392 } 435
		126	478 }
20.iv.54 ..	1	95	308
26.iv.54 ..	2	84	416
3.v.54 ..	3	6	489
10.v.54 ..	4	21	250
17.v.54 ..	5	54	341
26.v.54 ..	6	2	266
31.v.54 ..	7	91	319
7.vi.54 ..	8	43	214
14.vi.54 ..	9	34	198
21.vi.54 ..	10	26	187
28.vi.54 ..	11	?	151
5.vii.54 ..	12	23	138
12.vii.54 ..	13	94	158
19.vii.54 ..	14	88	186
26.vii.54 ..	15	73	188
3.viii.54 ..	16	74	179
10.viii.54 ..	17	66	126
20.viii.54 ..	18½	54	218
23.viii.54 ..	19	14	272
30.viii.54 ..	20	4	52
6.ix.54 ..	21	78	112
13.ix.54 ..	22	38	202
20.ix.54 ..	23	33	176
28.ix.54 ..	24	25	113
2.x.54 ..	24½	72	84
11.x.54 ..	26	70	97
18.x.54 ..	27	60	101
25.x.54 ..	28	44	99
1.xi.54 ..	29	65	89
8.xi.54 ..	30	87	120
15.xi.54 ..	31	96	176
		35[a]	166 } 122·5
		36[b]	99 }
		37[c]	133 }
		55[d]	92 }

[a] *Camponotus* spp. crossing
[b] [d] *A. longipes* crossing
[c] No ants crossing.

Bands made on 12.iv.54, and pinned around coconut palms at Mazizini, Zanzibar. Sample bands selected for analysis at random at approximately weekly intervals.

bands presumably killed all these foraging ants within 72 hours, since only very occasional ants were seen to cross the bands after 72 hours, and very numerous dead ants were visible round the palm trunks and at the nest entrances during this period. It became difficult to find the affected species in the neighbourhood of the banded palms, of which some 70 remained free from these species from 12th April 1954, when the experiment was started, to 10th November 1954, a period of seven months. Heavy rains fell in April and May, and the paper strips were regularly soaked; heavy storms occurred again in October and November. Table II gives the results of the DDT analyses of these bands. It will be seen that there is a large variation of DDT content on the freshly made bands. No smaller-sized species of ants, such as *Pheidole* spp., *Paratrechina longicornis* or *A. longipes*, crossed the bands until the second week in October, when *A. longipes* was found regularly crossing two of the bands, numbered 36 and 55.

The area where the crossing took place was marked and analysed and the DDT content was found to be below 100 μg./sq. cm. Other bands had fallen below this figure without the ants crossing but this is probably due to the fact that the presence of the bands had cut off the ants from their major food supplies and so had very considerably reduced their numbers.

TABLE III.

DDT content of paper bands treated with 10 DRDK and exposed in the laboratory.
(Analysis carried out by Dr. J. T. Martin.)

Date	Approx. no. weeks exposed	Band no.	Mean content (μg. total DDT per sq. cm.)
12.iv.54 ..	0	125 126	392 478 } 435
3.v.54 ..	3	A	541
7.vi.54 ..	8	B	496
5.vii.54 ..	12	C	360
3.viii.54 ..	16	D	370
6.ix.54 ..	21	E	393
2.x.54 ..	25	F	296
1.xi.54 ..	29	G	282

Bands made on 12.iv.54, and kept hanging in exposed (windy) position in the laboratory. A similar band prepared on 26.vi.53, using the same formulation, gave a mean DDT content, on 26.v.54, 11 months later, of 319 μg. per sq. cm.

Large-sized species of ants had crossed the bands from the day these had been put up. Practically all the bands were crossed regularly by *Camponotus rufoglaucus* (Jerd.) and *C. maculatus* (F.), and some by *C. vividus* (F. Sm.) and *Occophylla*. *Pheidole* sp. was not observed crossing the bands, after the initial kill of this species, until January 1955, nine months after putting the bands out. These bands proved more effective than similar ones made by dipping the same type of paper in concentrated Dieldrex (an emulsifiable oil containing 1·5 lb. dieldrin per U.S. gal.); the best of the latter were only effective for 3–4 months.

The loss of DDT from similar bands kept in the laboratory, exposed to wind, but shielded from sun and rain, was very much less (see Table III). In seven months, only about one-third of the DDT content had gone, and some of these bands were still lethal 30 months later to mosquitos (*Culex pipiens fatigans* Wied., *Aëdes aegypti* (L.)) and flies (*Lucilia sericata* (Mg.), *Stomoxys calcitrans* (L.)).

Persistence of the formulation on vegetation in the open varies with the type of vegetation. If sprayed on the trunks of coconut palms, 10 DRDK is effective against the small species of ants for at least six months but if applied to the trunks in times of drought, it causes "burns"; to avoid this, the treated paper-band technique was developed. When painted on coconut leaves, the formulation persists and is effective against *P. wayi* * and small species of ants for three to five weeks. Analysis for DDT on leaves taken at random in an area sprayed at 2 gal. per acre by a small air-mist sprayer (the Micron Sprayer) † showed deposits of 51 and 26 μg. DDT per sq. cm. after one week, and 29, 47, and 56 μg. DDT per sq. cm. four weeks after spraying. Although a considerable number of analyses of residual deposits of DDT from leaves, nut calyces and filter papers placed in the crowns of palms have been carried out by the kindness of Dr. Martin and of the chemists attached to the Colonial Pesticides Research Unit (C.P.R.U.) at Arusha, Tanganyika, the results show such variation, due to the many factors involved, that no definite conclusions can yet be drawn other than that DDT is deposited on all palms whatever their height and persists for several weeks. More investigation is required, and is being carried out by the C.P.R.U. It may be noted that the coconut grows outwards from the calyx and so the area on the nut that is free from insecticide extends daily. Since the palm produces its crop continuously, a new inflorescence opening, on an average, every 21 to 23 days, the advantages of sprays that give residual deposits tend to be nullified by the opening of new inflorescences, which are more attractive to *Pseudotheraptus wayi* than the older (sprayed) ones.

The formulation 10 DRDK has been applied as an air-assisted mist spray, in droplets up to 150 μ diameter, to a large number of tropical crop plants, and, provided that the dosage did not exceed one gallon per acre, no harmful effect was seen on any of them except cacao, which showed "burning" of the young leaves in patches, chillies (*Capsicum*), which showed slight spotting of young leaves, and the cucurbits tested (melon and cucumber), which were badly damaged. Various degrees of "burning" occur if the dosage exceeds one gallon per acre.

Selectivity of Residual Deposit.

An unexpected property of the formulation 10 DRDK is that its residual deposit is selective in its kill of various species of ants, and possibly of other insects. It has been used during 1953–1956, inclusive, in large-scale field experiments on the control of *P. wayi*. In the early experiments, it was hand-sprayed on the inflorescences and bunches of nuts of the palm; later, this method was superseded by the use of an air-mist spraying machine (the Micron Sprayer). In two experimental areas at Chukwani, Zanzibar, with a total of just over 1,000 bearing palms, 10 per cent. of the palms had *Oecophylla* nesting in them in October 1952. These areas were sprayed with a commercial formulation containing DDT from November 1952 to June 1953, and the percentage fell to 2·5. From June 1953 to January 1954 the area was hand-sprayed with 10 DRDK, and by October 1953 the percentage colonised by *Oecophylla* had increased to seven. During 1954, the area was machine-sprayed with the same formulation, and by October 1954, *Oecophylla* colonies were present in 15·1 per cent. of the palms, and by February 1955, in 38 per cent. The control area, a mile away, had originally 23·5 per cent. of its palms colonised by *Oecophylla*; here too there was

* Evidence will be presented in further papers in this series, showing that 10 DRDK is lethal to *P. wayi* when applied at 0·5 gal. per acre in aerosol form, or at 3·0 gal. per acre so as to leave a residual deposit.

† The machine was run up and down the rows of palms, and the insecticidal mist blown up between them. The insecticide does not get evenly distributed by this method and the palm leaves pick up higher dosages than might be expected.

TABLE IV.

Mortality of various instars of *P. wayi* to which a given size of droplet of 10 DRDK was applied. Controls were treated with droplets of distilled water.

Instar tested and condition	Droplet size (μ)	Where applied	Treated				Controls				% Diff.
			No. of tests	No. of individuals used	No. dead 48 hours later	%	No. of tests	No. of individuals used	No. dead 48 hours later	%	
Adult ♂♂ ..	85	S	3	23	23	100	3	20	0	0	
,, ,, ..		D	2	37	37	100	2	27	0	0	
Adult ♀♀ ..		S	2	9	9	100	2	9	1	11·1	
,, ,, ..		D	2	35	35	100	2	35	2	5·7	
V ..		S	1	10	10	100	1	15	0	0	
,, ..		D	1	5	5	100	1	5	0	0	
Late IV ..		D	1	20	20	100	1	5	0	0	
IV (fed) ..		D	1	10	10	100	1	5	0	0	
Early IV ..		D	1	4	4	100	1	5	0	0	
III ..		D	1	6	6	100	1	5	0	0	
II ..		D	1	12	12	100	1	12	2	16·7	
Total ..		—	16	171	171	100	16	143	5	2·9	97·1
Adult ♂♂ ..	75	D	1	13	13	100	1	12	1	8·3	
Adult ♀♀ ..		S	2	20	20	100	2	20	2	10·0	
,, ,, ..		D	1	15	14	93·3	1	15	2	13·3	
Late IV ..		D	1	10	10	100	1	7	0	0	
IV (fed) ..		D	1	5	5	100	1	5	0	0	
Total ..		—	6	63	62	98·5	6	59	5	8·5	90·0
Adult ♀♀ ..	60	S	1	8	8	100	1	8	0	0	
,, ,, ..		D	2	23	20	87·0	2	20	1	5·0	
Late IV (hungry)		D	1	9	9	100	1	5	0	0	
IV (fed) ..		D	1	10	8	80	1	10	0	0	
Early IV (fed)		D	1	12	10	83	1	10	0	0	
III ..		D	1	5	5	100	1	8	0	0	
II ..		D	1	4	4	100	1	5	0	0	
Total ..		—	8	71	64	90·0	8	66	1	1·5	88·5

Adult ♂♂ ..	50	S	2	20	20	100	2	40	2	2·5	
" " ..		D	3	38	28	73·8	3	29	1	3·4	
Adult ♀♀ ..		S	3	24	23	95·8	3	20	2	10·0	
" " ..		D	5	43	30	69·8	5	35	2	5·7	
V ..		D	2	15	4	26·7	2	15	1	6·7	
Late IV (hungry)		D	1	10	7	70·0	1	10	0	0·0	
Late IV (fed) ..		D	1	10	5	50·0	1	10	1	10·0	
Early IV (fed)		D	1	20	15	75·0	1	10	0	0·0	
III ..		D	1	10	10	100·0	1	8	0	0·0	
II ..		D	1	4	4	100·0	1	4	1	25·0	
Total ..		—	20	194	146	75·3	20	181	10	5·5	69·8
III ..	40	D	1	10	7	70·0	1	20	3	15·0	
II ..		D	1	6	6	100·0	1	5	0	0·0	
Total ..		—	2	16	13	81·2	2	25	3	12·0	69·2
Adult ♂♂ ..	30	S	5	25	12	48·0	5	25	5	20·0	
Adult ♀♀ ..		S	6	34	9	26·5	6	30	6	20·0	
IV		D	4	20	8	40·0	4	20	2	10·0	
III		D	10	50	32	64·0	10	50	5	10·0	
II		D	15	60	55	91·7	15	60	8	13·3	
Total ..		—	40	189	116	61·4	40	185	26	14·0	47·4
III	20	D	4	50	10	20·0	4	50	7	14·0	
II		D	3	30	24	80·0	3	30	2	6·7	
Total ..		—	7	80	34	42·5	7	80	9	11·2	31·3
Grand total	—	—	99	784	606	77·4	99	739	59	8·0	69·4

S = droplet applied laterally on thorax. D = droplet applied dorsally on thorax.

a slight but steady increase, and by January 1955, 36 per cent. of the palms were so colonised. The increase of *Oecophylla* in the sprayed area might well have been due to natural factors, but whatever the cause of the increase, the experiment demonstrated that the insecticidal formulation used had no adverse effect on the population of *Oecophylla*.

In other sprayed areas, the results have been even more noticeable. At Mazizini, in January 1953, there was no *Oecophylla* in the area, 90 per cent. of the palms being foraged by *A. longipes* and 65 per cent. having this ant nesting in débris in the crowns. In addition, 5–10 per cent. of the palms had *Pheidole* nesting in the crowns or foraging from the ground. Machine-spraying of 10 DRDK was undertaken in eight plots of 8–12 acres each. The amount of insecticide applied, frequency of application, and mean droplet size varied in these different experiments. In one plot, where a total of 10 gallons 10 DRDK per acre was applied in sprays with a droplet size of 80–90 μ in 12 applications during the year, the proportion of palms occupied by *Oecophylla* colonies increased from nil to 21·7 per cent. After a second year's spraying, with an increased total dosage of 10 DRDK (33 gal. per acre in 12 applications at a mean droplet size of 70–80 μ) the proportion of palms with *Oecophylla* colonies had increased by March 1955 to 26·1 per cent., while *A. longipes* and *Pheidole* had been eradicated from the ground, and the colonies in the palms had been reduced to 7·5 per cent. In the third year, a total of 30 gal. per acre was applied in nine applications at the same mean droplet size; the proportion of palms with *Oecophylla* colonies increased to 30 per cent. by April 1956, whereas those colonised by *A. longipes* decreased to 1·5 per cent. The species of ants were recorded individually for each palm at six-monthly intervals, and in this area there was very little movement of *Oecophylla* colonies from palm to palm. In other experimental blocks, where DDT formulated as a wettable powder, and formulations containing lindane or dieldrin, have been used, there has been a very considerable movement of *Oecophylla* colonies from palm to palm.

In these areas sprayed with 10 DRDK, there has been no noticeable increase in aphids, mealybugs or scale insects. Populations of honey-bees, of which the major species are *Apis mellifera* L. var. *adansonii* (Latr.), *Hypotrigona* spp. and *Trigona* spp., have increased in number of colonies and individuals. The formulation was effective in controlling *P. wayi* (see footnote, p. 157), *Diocalandra frumenti* (F.), and a Pyralid borer, *Lamoria* sp., and there has been a decrease in the number of palms damaged by *Orcytes* spp.

In the control area, *A. longipes* remained dominant, no *Oecophylla* became established and the numbers of other insects remained unchanged, apart from the usual seasonal variations.

Lethal Dosage for *P. wayi*.

It has proved impossible to obtain large numbers of either adults or nymphs of *P. wayi*. Individual nymphs or adults can be kept quite easily in the laboratory, but they repel one another and if more than two or three are kept together in a cage the majority die from starvation. Supplies of food are a considerable problem. Two to four individuals can be reared in a sleeve around a coconut-palm inflorescence but this method does not lend itself to rearing large numbers, unless a great deal of labour is available, owing to the height of the palms and the slowness of moving ladders around. Collecting nymphs of *P. wayi* in the field is also slow and expensive and individuals are often damaged during the process. It has not been possible to collect sufficient numbers to carry out normal bioassays, but some 1,500 individuals have been used in a series of tests that indicate what is the minimum droplet size most likely to give 100 per cent. kill of the most resistant stages.

The technique described by Kerr (1954) was used to ascertain the lethal dose of 10 DRDK in droplet form. Table IV gives a summary of the tests carried out. The data are insufficient for a graph, but suggest that the lethal dose varies with the instar. It was found that the minimum amount required to be certain of killing an old adult (one of the less susceptible stages, see Table V), was one 85-μ droplet applied to the dorsal surface of the thorax or abdomen, or a 60-μ droplet applied laterally. An 85-μ droplet contains 0·31 μg. DDT.

The dosage required to give a lethal residual deposit was tested by spraying glass petri dishes with known amounts of the formulation and allowing nymphs in the various instars and adults of *P. wayi* to walk about on these for one minute. Control insects were placed in clean petri dishes for equivalent periods. The lethal dosage was taken as the minimum of those tested that gave complete kill of all stages within 48 hours of application, which was 2·7 mg. p,p′DDT per sq. ft. The data are summarised in Table V. Freshly moulted individuals appeared more susceptible than older ones in the same instar.

Variation of Formulation.

It was considered that the addition of lindane, to a concentration of 0·1 per cent., might enhance the lethal effects of the formulation. Experiments were carried out with lindane included in the formulation to give concentrations of 0·1, 0·5 and 1·0 per cent., the formulation then being sprayed at one gallon per acre over an 18-acre coconut plantation. With lindane at 0·1 per cent., the formulation was no longer selective as regards ants and gave a poorer control of *P. wayi* than did the original formulation. With lindane at 0·5 per cent., it was likewise not selective as regards ants, and various Homoptera increased rapidly, due to the reduction of their predators and parasites; it also gave no better control of *P. wayi* than did the original formula. With lindane at 1·0 per cent., the formulation behaved no differently from 1·0 per cent. lindane in oil without DDT and coumarone resin; it gave an extremely good kill of *P. wayi* and all insects other than mealybugs or scale insects, which increased very considerably, and it reduced the numbers of *Oecophylla* even more than those of other species of ants. This last effect is due to the habits of *Oecophylla*, with its leaf nests, and the fumigating action of lindane, which the ground-nesting ants tend to escape. Lindane applied in a spray at 1·0 per cent. in coconut plantations gave residual effects for about 10 days only, and the residual effects of 10 DRDK are spoilt by the additional lindane since small rhombic crystals of DDT are obtained instead of needle-like ones. The addition of lindane is thus detrimental to this formulation.

The addition of dieldrin to give concentrations of 0·1, 0·5 and 1·0 per cent. has also been tested. Dieldrin at 0·1 per cent. increased the residual persistence of the formulation but lowered its selectivity. The behaviour of the formulation still more closely resembled that of dieldrin with increasing dosages of the latter. This insecticide has been found unsuitable for this work.

Several other insecticides have been added to give concentrations of 0·1, 0·5 and 1·0 per cent. These include rotenone, pyrethrins and endrin. None of these showed any advantage and, in most cases, the formula was less effective with the additional insecticide than without it.

Summary.

An undesirable effect of using a dust containing 0·4 per cent. lindane for the control of *Pseudotheraptus wayi* Brown on coconut palms is the eradication of *Oecophylla longinoda* (Latr.), a species of ant inimical to this Coreid, and in the

TABLE V.

Mortalities of various stages of *P. wayi* after walking about for one minute on known deposits of DDT.

Instar tested and condition	Mean deposit (mg. p,p′ DDT per sq. ft.)	Treated			Controls		
		No. tested	No. dead 48 hours later	%	No. tested	No. dead 48 hours later	%
Adult ♂♂	2·7	8	8	100	10	1	10·0
Adult ♂♂ (freshly emerged)		4	4	,,	4	0	0·0
Adult ♀♀		12	12	,,	15	0	0·0
Adult ♀♀ (freshly emerged)		6	6	,,	9	2	22·2
V		8	8	,,	12	1	8·3
IV		15	15	,,	20	2	10·0
IV (freshly emerged) ..		5	5	,,	—	—	—
III		55	55	,,	50	3	6·0
II		50	50	,,	50	6	12·0
Total		163	163	100	170	15	8·8
Adult ♂♂	1·6	12	9	75·0	15	1	6·7
Adult ♂♂ (freshly emerged)		6	6	100·0	4	0	0·0
Adult ♀♀		14	7	50·0	16	0	0·0
Adult ♀♀ (freshly emerged)		9	9	100·0	8	1	12·5
V		13	10	77·0	12	1	8·3
V (freshly emerged) ..		5	5	100·0	6	0	0·0
IV		17	13	76·5	15	0	0·0
IV (freshly emerged) ..		10	10	100·0	10	1	10·0
III		48	35	73·0	45	5	11·1
II		50	48	96·0	50	7	14·0
Total		184	152	82·6	181	16	8·8
Adult ♂♂	0·7	5	1	20·0	5	0	0·0
Adult ♂♂ (freshly emerged)		6	2	33·3	7	1	14·3
Adult ♀♀		8	2	25·0	9	1	11·1
Adult ♀♀ (freshly emerged)		5	3	60·0	4	0	0·0
V		9	2	22·2	11	1	9·1
IV		21	9	42·9	28	4	14·3
IV (freshly emerged) ..		16	6	37·5	10	2	20·0
III		54	27	50·0	85	17	20·0
II		72	51	70·8	81	20	24·7
Total		196	103	52·6	240	46	19·1

search for a more suitable preparation, formulations were tested in Zanzibar that contained DDT, with synthetic resins to prevent its absorption through the treated surface of the palm. One such formulation, prepared by dissolving 23·5 lb. of a proprietary coumarone indene resin and then 235 lb. 80 per cent. p,p'DDT in a mixture of 100 gal. power kerosene and 100 gal. diesoline, heated to 40–45°C., is here termed 10 DRDK and its properties described.

When 10 DRDK was applied by pneumatic hand-sprayers to the centres of palm crowns, small species of ants (*Pheidole* spp., *Crematogaster* spp., *Paratrechina longicornis* (Latr.)) and *Anoplolepis longipes* (Jerd.) were eradicated from such sites, whereas *O. longinoda* increased in numbers and other large species (*Camponotus* spp., *Polyrhachis* spp., etc.) were unaffected. Although 10 DRDK was lethal to all species when applied as an aerosol in the laboratory, the residual deposit from it killed only the smaller species, apparently because their bodies make contact with the DDT crystals whereas those of the larger species (except *A. longipes*) are held clear. Under Zanzibar conditions, this deposit, which is at first gummy, gives rise within 2–3 weeks, or following mechanical disturbance, to needle-like crystals of DDT, 10–120 μ long × 2–10 μ wide projecting from the sprayed surface and forming clumps up to 1·5 mm. high.

In field tests, paper bands dipped in 10 DRDK and attached round palm trunks prevented the passage of *A. longipes* for six months, and of *Pheidole* for nine months, despite heavy rain; that of the larger species of ants was unaffected. Determinations of the deposit on a sample band selected each week at random showed great variability but fell from 392–478 μg. DDT per sq. cm. initially to 92–176 μg. after 31 weeks. In concurrent tests of similar bands exposed in the laboratory, the deposit fell only to 282 μg. per sq. cm. over approximately the same period.

In tests of 10 DRDK applied topically to the dorsum of *Pseudotheraptus wayi*, complete mortality of adults was obtained within 48 hours with droplets 85 μ in diameter (containing 0·31 μg. DDT) and the size required diminished progressively, the earlier the stage treated. When individuals of *P. wayi* were allowed to walk for one minute on glass plates bearing known deposits from 10 DRDK, complete mortality of all stages, from 2nd-instar nymphs to adults, followed within 24 hours of exposure to 2·7 mg. DDT per sq. ft., but not to 1·6 mg., except in the case of recently moulted adults, 5th- or 4th-instar nymphs.

Two experimental areas totalling some 1,000 palms, of which 10 per cent. had *Oecophylla* nesting in them in October 1952, were sprayed with a commercial formulation containing DDT from November 1952 to June 1953, and the percentage fell to 2·5; the areas were then treated with 10 DRDK by hand-sprayer until January 1954 and by machine for the rest of 1954. The percentage of palms having *Oecophylla* in October 1953, October 1954 and February 1955 increased to 7, 15 and 38, respectively. In a control area one mile away, the percentage rose from 23·5 to 36 over the same period. In a third area, 12 applications of 10 DRDK totalling 10 gal. per acre were made by machine during 1953, 12 totalling 33 gal. in 1954 and 9 totalling 30 in 1955, and the percentage of palms colonised by *Oecophylla* rose from nil to 21·7 in 1953, to 26·1 by March 1955 and to 30 by April 1956, while the percentage colonised by *A. longipes* fell over the same period from 90 to 1·5. In the control areas, *A. longipes* remained dominant and no *Oecophylla* became established.

The addition of lindane to 10 DRDK to give concentrations of 0·1, 0·5 or 1·0 per cent. adversely affected the selective properties of the formulation, and although the highest strength gave a good kill of *P. wayi* and other insects, apart from Coccids, which increased considerably, it reduced *Occophylla* to a greater extent than it did other species of ants. No advantages are obtained by the addition of dieldrin, endrin, pyrethrins or rotenone.

Acknowledgements.

I wish to thank Dr. J. T. Martin of the Horticultural Research Station, Long Ashton, England, and Dr. Robinson of the Colonial Insecticides Research Unit, Arusha, Tanganyika, for their help and their analyses of DDT contents and residues; and also the manufacturers of various resins for their help and for samples, particularly The British Resin Products Ltd., makers of "Epok" coumarone indene resin. I also wish to thank Mr. L. J. Stevens, who supervised a large number of the field experiments and prepared the insecticidal formulations that were used, and my subordinate staff who carried out without complaints the unpleasant task of spraying, Mr. A. K. Briant, O.B.E., Director of Agriculture, Zanzibar, for permission to publish this paper, and Mr. G. E. Tidbury and Mr. R. K. Tremlett for their help in its preparation.

References.

Kerr, R. W. (1954). A method for the topical application of small measured doses of insecticide solutions to individual insects.—*Bull. ent. Res.* **45** pp. 317–321.

Lewis, C. T. (1954). Studies concerning the uptake of contact insecticides. I. The anatomy of the tarsi of certain Diptera of medical importance.—*Bull. ent. Res.* **45** pp. 711–722.

Parkin, E. A. & Green, A. A. (1945). Residual films of DDT.—*Nature, Lond.* **155** p. 668.

Parkin, E. A. & Green, A. A. (1947). DDT residual films. I. The persistence and toxicity of deposits from kerosene solutions on wall-board.—*Bull. ent. Res.* **38** pp. 311–325.

Potts, W. H. & Vanderplank, F. L. (1945). Mode of entry of contact insecticides.—*Nature, Lond.* **156** p. 112.

van Tiel, N. (1952). Improvement of the residual toxicity of DDT solutions by the addition of coumarone resin.—*Bull. ent. Res.* **43** pp. 413–419.

van Tiel, N. (1955). Influence of resins on crystal size and toxicity of insecticidal residues.—Ph.D. thesis, Univ. Leiden.

Van den Brande, J., Van den Hende, A. & Jacobs, T. (1951). L'influence du solvant sur l'efficacité des solutions de DDT.—*Proc. II int. Congr. Crop Prot. 1949* **2** pp. 453–461.

Vanderplank, F. L. (1947). Experiments with DDT on various species of tsetse flies in the field and laboratory.—*Trans. R. Soc. trop. Med. Hyg.* **40** pp. 603–620.

Vanderplank, F. L. (1959). Studies on the coconut pest, *Pseudotheraptus wayi* Brown (Coreidae), in Zanzibar. II. Some data on the yields of coconuts in relation to damage caused by the insect.—*Bull. ent. Res.* **50** pp. 135–149.

Way, M. J. (1951). An insect pest of coconuts and its relationship to certain ant species.—*Nature, Lond.* **168** p. 302.

Way, M. J. (1953). Studies on *Theraptus* sp. (Coreidae); the cause of the gumming disease of coconuts in East Africa.—*Bull. ent. Res.* **44** pp. 657–667.

© Commonwealth Agricultural Bureaux, 1959.

STUDIES ON *STOMOXYS CALCITRANS* (L.) IN UGANDA, EAST AFRICA.

I.—A METHOD OF REARING LARGE NUMBERS OF *STOMOXYS CALCITRANS*.

By H. C. M. Parr.*

For many years it has been realised that certain species of *Stomoxys* constitute a major pest of cattle in Uganda not only because they are suspected of mechanically transmitting trypanosomiasis, but also on account of their nuisance value. In many areas in Uganda where the incidence of *Stomoxys* is high, grazing of cattle is seriously interrupted by the numerous and painful bites which these insects inflict. It is generally accepted that this leads to a severe loss in milk yield, and in beef animals and in calves particularly, to a considerable loss in weight and to general debility.

In parts of Uganda where large herds of locally owned cattle exist and where there is a high incidence of *Stomoxys*, farmers have developed a system whereby their cattle are kept in sheds with a smudge fire burning during the hot sunny period of the day when the biting activity of the flies is at a maximum. Consequently, the animals are only grazed during the early morning and in the evening. Again, it is believed that this leads to a loss in milk yield and of weight in beef cattle. In other parts of Uganda, for example in the Karamoja District, the severe interference with grazing of the animals by biting flies causes the Karamojong to drive their herds many miles to less suitable and inferior grazing areas free from biting flies.

Adults of *Stomoxys* can be found throughout the whole of the Uganda Protectorate, their numbers being greater during and immediately following the rainy periods. So far the author has identified only two species, namely *S. calcitrans* (L.) and *S. nigra* Macq., with *S. calcitrans* the dominating species. For the purpose of this work, therefore, it was decided to concentrate on *S. calcitrans*.

In order to study in detail the behaviour and life-history of *S. calcitrans*, both under laboratory conditions and in the field, it was decided that a suitable method of breeding the insect under laboratory conditions should first be evolved. The present paper deals only with the method and techniques of rearing the insect.

Materials and Methods.

The methods of rearing *Stomoxys* devised by Doty (1937) and by Eagleson (1943) have not proved suitable under the conditions which prevail in East Africa, and egg production and adult emergences were insufficient to maintain a large enough stock colony.

Cages.

Oviposition cages for the adults were composed of a frame of painted angle-iron measuring approximately 2 ft. × 2 ft. × 2 ft. These cages were built in batteries in a line of four, thus economising in material by having a common wall between each cage and the next adjacent. A three-ply wood flooring was fitted

* Colonial Pesticides Research Unit, Arusha, Tanganyika (in collaboration with the Animal Health Research Centre, Department of Veterinary Services and Animal Industry, Uganda).

six in. from the base, and a length of three-ply wood was fitted along the front of the battery rising from the floor to a height of 10 in. and forming part of the front wall of the cage. Originally the rest of the walling of the cages was of wire-mesh gauze, but this resulted in a heavy death-rate of flies due to buffeting against the hard wire. The wire gauze was then replaced by cotton mosquito netting, which considerably reduced the numbers of deaths. This in turn had to be replaced by a smaller mesh sandfly netting, owing to the ability of the young soft-bodied flies to squeeze through the larger mesh of the mosquito netting.

To enable the hand to be inserted, holes, 9 in. in diameter, were cut in the three-ply wood along the front of the cages. These were fitted with sandfly netting sleeves, 12 in. long.

Maintenance of adults, and egg production.

Each cage contained approximately 1,200 flies and in order to offset the reduction in numbers resulting from mortality, 1,000 freshly emerged flies were added daily.

Food for the adults consisted of 0·2 per cent. citrated bullocks' blood soaked into portions of highly blood-absorbent pads which were then hung from the roof of the cage. Blood was supplied daily at 8 a.m. and again at 4 p.m., and the adults gorged readily. Blood soaked into gauze in petri dishes placed on the floor of the cage proved unsatisfactory, inasmuch as the flies appeared incapable of locating the food, and the few that did survive tended to deposit their eggs in it, from which it was impossible to extricate them. Blood was collected once per week in 10-ml. vials and kept in the refrigerator until needed.

The medium used to induce egg production was originally composed of a mixture of the following ingredients:—3 oz. grass meal, 3 oz. oatmeal, 6 oz. dried meat granules, 2 oz. sugar and 1 tablespoonful of malt and barley extract. These ingredients were mixed with sufficient distilled water to make the medium just so damp that no free water could be expressed when a portion was squeezed in the hand, since it was noticed that too much moisture proved fatal to the first and second larval instars. The thoroughly mixed medium was then placed in tin containers and securely covered with fine cheese cloth and allowed to ferment for 2–3 days until the heat generated had become reduced, and the medium had taken on a strong smell of ammonia.

This medium proved unsatisfactory for the following reasons and had to be replaced. The addition of oatmeal failed to produce a loose texture and many deaths occurred during the first and second larval stages due to packing-down of the medium. In addition, the cost of buying or of making dried meat granules in the laboratory was prohibitive. Furthermore, dried meat is palatable to the African.

The following medium has, however, proved extremely satisfactory:—9 oz. dried cow dung, 5 oz. dried blood granules and 1 oz. sugar. The partially dried dung was collected and allowed to dry out completely at room temperature and was then crushed. The blood granules were made by collecting bullocks' blood from the abattoir and steaming it for 20 minutes and then allowing it to dry out at room temperature, or in an oven at 70°C. (*cf.* Bredon, Juko & Marshall, 1957). Fermentation of the medium was allowed to take place in covered containers. When fermentation was complete and the heat generated had subsided, portions were placed in shallow circular trays 6 in. in diameter and 1 in. in depth. The trays were then introduced into the cages and supported on 4-in. high platforms placed on the floor of the cages. Eggs were readily deposited by gravid females within this medium to a depth of $\frac{1}{8}$ to $\frac{1}{4}$ in. below the surface.

The trays were removed daily from the cages and their contents split into portions and placed in either 1-lb. or 2-lb. Kilner jars. These jars were then

filled up to within 1 in. of the top with a further quantity of exactly the same medium. The tops were covered with squares of *Americani* * cloth secured by elastic bands and the jars were then placed in the constant-temperature and humidity room described below.

The cages containing adults were kept under ambient atmospheric conditions on a laboratory bench facing a well lighted window. Mating and oviposition readily occurred and took place at all times during daylight hours.

Rearing of larvae and pupae.

In order to provide conditions for rearing larvae, similar to those occurring in nature, a constant-temperature and humidity room was constructed (hereafter referred to as the C.T. and H. room). It was assumed that a fairly high soil temperature and humidity would be essential for the development of the eggs, larvae and pupae, and that complete darkness would be an important factor. Consequently, a windowless room, 18 ft. × 6 ft. and 12 ft. high with walls of cement blocks, 9 in. thick, was constructed. The walls and ceiling were treated with a coat of dark-coloured, waterproof, bituminous paint, in order to prevent excessive loss of atmospheric humidity by absorption into the walls. A coat of silver bituminous paint was then applied in order to give as much reflected light as possible whilst anyone was actually working in the C.T. and H. room.

The room was heated by a series of tubular heaters installed at a height of 1 ft. from floor level around all four walls. These heaters were connected to the conventional type of wall-mounted thermostat, with a hot-wire relay vacuum switch incorporated in the circuit to prevent excessive "arcing" of the contact points within the thermostat. Without the relay vacuum switch it was found that "arcing" did occur, and the thermostat failed to function satisfactorily on account of excessive overheating.

Regular records over a period of many months have shown that the temperature within the medium in the breeding jars has never fallen below that of the atmosphere in the C.T. and H. room by more than 1°C.

Humidity was produced by using a 1-kilowatt electric-kettle element to heat a volume of 1½ pints of water in a circular metal container 6 in. in diameter. The depth of the water was maintained at a level just sufficient to cover the heater, any loss in volume through evaporation being automatically replaced from a 10-gallon copper reservoir.

The fact that the volume of water to be heated by the 1-kilowatt heater was always maintained at 1½ pints ensured rapid heating and consequent rapid evaporation of water from a surface area of approximately 27 sq. in.

The heater in the humidifier was controlled by a wall-mounted hygrostat with a double hot-wire relay vacuum switch wired into the circuit. If by any chance the humidity inside the room rose above the pre-set value, then an exhaust fan, installed in the top of one of the walls, automatically came into operation, drawing drier air into the room from the outside atmosphere.

Installed in the roof of the C.T. and H. room was a long-bladed electric fan, which was set to revolve slowly at approximately 30 revolutions per minute in order to circulate air inside the room.

The framework of the shelving was composed of a proprietary make of painted angle-iron and the shelving itself of ¼-inch mesh, stout, galvanised coffee wire in order to prevent "pocketing" of the atmosphere between the shelves (which would have occurred if solid shelving had been used).

The C.T. and H. room was set to run at a temperature of 90°F. and a relative humidity of 90 per cent. Variation in temperature was ±1°F. and relative humidity ±2 per cent.

---

* Local terminology for a loose-weave cotton cloth.

The jars containing the newly laid eggs were placed in the C.T. and H. room, where they needed no further attention. After approximately ten days, the final larval instars migrated to the surface of the medium and pupated either on the surface or down to a depth of 1 in. The top layer of the medium was then shaken out on to filter paper and the pupae picked off with entomological forceps. The pupae were then placed in shallow trays which were introduced into a 1-ft.-cube emergence cage of sandfly netting, the netting being supported only by a simple wire framework. Again it is important to use sandfly netting and not mosquito netting, on account of the ability of the soft-bodied newly-hatched flies to squeeze through the mesh of the latter.

On emergence, the flies were kept in the C.T. and H. room for three to four hours to enable their wings to expand and their body chitin to harden and were then transferred to the battery of oviposition cages.

A preliminary experiment was carried out to find the possible effects of overcrowding and consequent malnutrition of developing larvae. Exactly the same quantity of the same batch of medium was placed in two 1-lb. jars. Into one jar, 200 eggs were introduced and into the other, 400 eggs, and both jars were placed in the C.T. and H. room. After ten days' interval, both jars produced pupae, and 100 pupae from each jar were cleaned and accurately weighed. The weight of 100 pupae from the jar containing 200 eggs was 0·89 g., and that of the jar containing 400 eggs was only 0·42 g. It is most important to avoid overcrowding of the larvae in the jars, and only 200 and 400 eggs should be introduced into 1-lb. and 2-lb. jars, respectively.

In the routine running of the colony, it was impracticable to count 200 or 400 eggs for each jar. However, it was found that, if the population of flies in a cage were maintained at approximately 1,200, the trays containing the egg-laying medium removed once every 24 hours, and the medium evenly divided between 20 jars, then each jar eventually produced approximately 200 pupae. Only ten jars were required for each 24-hour output of eggs when 2-lb. jars were used.

At the time the colony was started it was well into the middle of the dry season and it was only possible to capture 33 wild examples of *S. calcitrans*. From these original 33 flies, the colony has grown and for almost two years has been maintained at an approximate strength of 5,000 flies.

Summary.

The importance of certain species of *Stomoxys* in Uganda, the possibility that these species may be responsible for the mechanical transmission of trypanosomiasis, and the effects of severe biting of *Stomoxys* on cattle causing loss in milk yields and weight in beef animals, is pointed out.

A satisfactory method is described for rearing large numbers of *Stomoxys calcitrans* (L.) under the conditions that prevail in East Africa.

A description of special cages for keeping the adults and for egg production is given, together with a technique for supplying the adults with 0·2 per cent. citrated bullocks' blood.

A satisfactory egg-laying and breeding medium contained 9 oz. of dried cow dung, 5 oz. of dried blood granules and 1 oz. of sugar.

A detailed description of the construction and working of a constant-temperature and humidity room for rearing larvae and pupae is given, the temperature and relative humidity of the room being maintained at 90°F. and 90 per cent., respectively.

The maximum number of eggs that can be introduced into 1-lb. and 2-lb. Kilner jars without causing overcrowding and subsequent under-nourishment in the later larval instars was found to be 200 and 400, respectively.

References.

BREDON, R. M., JUKO, C. D. & MARSHALL, B. F. (1957). Nutritional chemistry.—*Rep. Dep. vet. Serv. Uganda 1956* pp. 52–59.

EAGLESON, C. (1943). Stablefly.—*Publ. Amer. Ass. Advanc. Sci.* no. 20, pp. 77–78.

DOTY, A. E. (1937). Convenient method of rearing the stable fly.—*J. econ. Ent.* **30** pp. 367–369.

© Commonwealth Agricultural Bureaux, 1959.

A PRELIMINARY NOTE ON *HELOPELTIS* SPP. DAMAGING CASHEW IN TANGANYIKA TERRITORY.

By G. Swaine

Entomologist, Department of Agriculture, Arusha, Tanganyika.

(Plate IV.)

The cashew nut, *Anacardium occidentale*, industry has assumed considerable importance of recent years in the economy of Tanganyika Territory, production of unshelled nuts rising from approximately 5,500 tons in 1948 to 33,650 tons in 1957, valued at over £1,500,000 sterling. Continued increases can be expected for some time to come as extensive planting is still being carried out.

Helopeltis damage appears to have been first observed on cashew in Tanganyika by Mr. Leslie-Moore, a former Field Officer of the Agriculture Department, who reported young shoots of cashew at Kilwa, Southern Province, in September 1945, " showing what appeared to be Capsid bug damage ". Elsewhere, published records of *Helopeltis* on cashew are confined to Nigeria (Dr. W. J. Hall, private communication). Golding (1945) reported having seen breeding of *H. schoutedeni* Reut. (= *sanguineus* Popp.) on cashew at Ibadan, Nigeria. Unpublished information of E. O. Pearson (Dr. W. J. Hall, private communication), records large populations of all stages of a species of *Helopeltis*, believed to be *H. schoutedeni*, attacking cashew in the neighbourhood of Namapa, Mozambique, in June 1945 and another occurrence of an unidentified *Helopeltis* on cashew in Equatoria Province, Sudan. The first specimens of *Helopeltis* on cashew in Tanganyika, collected by the writer at Kisarawe, near Dar es Salaam, in June 1953, were described by Miller (1954) as a new species, *H. anacardii*. Subsequent collections have shown the presence of a second species, identified by Miller as *Helopeltis* sp. ? *bergrothi* Reut.

Distribution.

Cashew is grown, mainly by the African peasant farmer, in a coastal belt, 80–90 miles wide, and on the nearby island of Mafia. The main concentration is in the Southern Province in the Lindi and Masasi districts and along the Mtwara–Newala road.

Both species of *Helopeltis* have been found in the cashew areas around Dar es Salaam, Bagamoyo and Ruvu in Eastern Province, and on the odd trees occurring in the Morogoro district. In the Southern Province they have both been found along the Mtwara–Newala road and at Masasi and Mahiwa. In the important Mingoyo area, 15 miles from Lindi, and on Mafia Island, only *H. anacardii* has so far been observed, but it is probable that more extensive searches in these areas would reveal the presence of the second species also. *Helopeltis* damage has been observed on odd, isolated cashew trees growing near Tanga but no specimens of the insects were found at the time of inspection. Both species have been identified by the writer in specimens collected in August 1955 by Dr. F. L. Vanderplank on cashew in Zanzibar. *Helopeltis* is thus distributed widely throughout the cashew-growing areas and is likely to become of increasing importance as the industry expands and monocultural conditions of cultivation develop.

Life-cycles.

The life-cycles of both species were studied at the Coast Agricultural Station, Chambezi, Bagamoyo during June and July 1955. Adult insects were enclosed in muslin sleeves tied on to fresh terminal shoots of cashew and transferred daily to freshly bagged shoots. The date of laying of eggs in any one bag was thus known. Nymphs which emerged in bags left on the trees were transferred to freshly bagged shoots and examination made daily thereafter for the succeeding instar. This process was repeated for each instar until the life-cycle had been

TABLE I.

The lengths of stages in the life-cycle of *Helopeltis anacardii*. Chambezi, Bagamoyo, June–July 1955. Mean temperature 23·6°C.

Stage	Egg	Nymphal instars					Adult
		1st	2nd	3rd	4th	5th	
No. of individuals ..	135	93	60	53	40	31	8
Duration of stage (days) ..	15·2 (14–18)	4·5 (4–6)	3·2 (3–5)	3·7 (2–5)	3·6 (2–6)	5·7 (4–8)	17·5 (12–25)

Egg–adult, 35·9 days (29–48).

completed. It was found that a newly bagged terminal shoot remained suitable as food for about three days only, owing to the sucking damage caused by the nymphs. After this time the nymphs present in any one bag were transferred to a fresh terminal shoot. The durations of the various stages are given in Tables I and II.

TABLE II.

The lengths of stages in the life-cycle of *Helopeltis* sp. Chambezi, Bagamoyo, June–July 1955. Mean temperature 23·6°C.

Stage	Egg	Nymphal instars					Adult
		1st	2nd	3rd	4th	5th	
No. of individuals ..	204	40	52	56	44	47	14
Duration of stage (days) ..	16·1 (15–18)	4·2 (3–6)	4·1 (3–6)	4·1 (3–5)	3·8 (3–7)	6·9 (5–10)	17·6 (1–29)

Egg–adult, 39·2 days (32–52).

It was not possible to obtain information on the preoviposition period at Chambezi. The records of Kirkpatrick (1941) indicate that this would be approximately 12 days, giving a complete generation of *H. anacardii* as 48 days and that of *H. bergrothi* as 51 days. The adults of both species were relatively short-lived in the observations reported here (17 days, approximately). Patterson (1914) found adults of *H. bergrothi* in Ghana to live for at least 70 days on cacao pods.

The eggs are laid directly into the young green tissues, mostly on the terminal portions of the vegetative and flowering shoots, but sometimes also in the main

veins of recently opened leaves. The eggs themselves are completely concealed in the plant tissues, being recognisable externally only by projecting white cotton-like threads (chorionic processes), which are more conspicuous in the case of *Helopeltis* sp. than *H. anacardii*. The average number of eggs laid per day in experiments was 3·7 for *H. anacardii* (17 observations) and 3·4 for *Helopeltis* sp. (22 observations).

The newly emerged first-instar nymphs congregate together on the under-surface of a young leaf on which they feed by sucking. Little dispersion of individuals occurs until the third stage, when feeding may commence on the young, succulent stems. The first- to third-instar nymphs avoid the sun and always return immediately to a shaded position when deliberately exposed. Nymphs of the fourth and fifth instars are usually solitary and feed mainly on the stems rather than the leaves.

Nature of Damage.

The sucking of the young nymphs causes distortion and crumpling of the leaves, damage which is accompanied by the angular lesions along the veins characteristic of *Helopeltis* attack (Pl. IV, fig. 1). The repeated sucking of the older nymphs, and of the adults, results in the die-back of the terminal parts of the shoots. Frequently, sucking of the shoots results in the exudation of a clear gum from the damaged tissues which gradually hardens on exposure to the atmosphere. Where late nymphal populations are heavy (10 or more per tree in the case of a tree 1–2 years old), the terminal buds are killed before they are able to open. Subsequent growth, if it occurs, comes from numerous lateral axillary buds, and this gives rise to a witches' broom type of growth and general malformation of the tree (Pl. IV, fig. 2). The developing nuts are attacked by the older nymphs and adults; if attacked whilst very young, the nuts shrivel and die on the tree, frequently falling to the ground later as they dry out; older nuts are not killed but are reduced in size and show signs of damage in numerous pock-like marks in the fruit wall (Pl. IV, fig. 3). Further damage is also caused to the cashew apple, resulting in it shrivelling and drying out or in premature cracking of the outer skin developing from the cankerous spots caused by *Helopeltis* and the entry of moulds and of insects such as *Carpophilus* spp. and *Drosophila* spp. which hasten the process of decay.

Observations have indicated that damage is generally heavier in young trees (1–3 or 4 years old) than in more mature ones (8–14 years old). An isolated young tree, however, frequently escapes heavy damage, whereas, in a plantation of young trees, damage can be so severe that growth is almost prevented.

Where young trees are no longer available, *e.g.*, in an established plantation, a ' settled ' population of *Helopeltis* causes continuing damage to the older trees.

Seasonal Incidence.

The main growth of the cashew tree begins shortly after the end of the rains in May with the production first of vegetative, and later of flowering shoots. Towards the end of the rains and during the month of June, *Helopeltis*, and in particular, *H. anacardii*, is difficult to find; with the increase of material suitable for breeding and feeding presented by the new shoots, the insects rapidly become more numerous and can be obtained with ease from July to October–November when the crop matures. On older trees, the insects are relatively scarce from December until June but they are readily found on young trees in December to April as these trees are putting on a considerable amount of new and succulent growth during much of this period in addition to their main growth after June.

Effect on Crop.

Little information has been gathered to date on the yields, actual or potential, of trees of different ages and it is therefore impossible to give any estimate of the adverse effect of *Helopeltis* as a whole

Assessment of the effect on two varieties of two-year-old trees at Chambezi, Bagamoyo, was made during 1955 (Swaine, 1956, where the results of the work done in 1955 are summarised, and from which Tables IV and V have been derived). In one experiment, a three-acre block of Mozambique trees was marked off at the end of a compact block of nine acres and then sub-divided into six blocks, of which two were untreated controls, two received five applications of a 0·5 per cent. γ BHC dust and the remaining two received eight applications of a 0·5 per cent. γ BHC dust. The rate per application was 18 lb. per acre. In the absence of more suitable equipment, application was made by rotary hand-dusters fitted with long delivery pipes. In a second experiment, with Zanzibar cashew, a more spreading variety than the Mozambique, a compact two-acre block of trees was sub-divided into three smaller blocks, of which one was untreated control and the other two received 14 applications during the growing season of a 5 per cent. DDT dust and a 0·5 per cent. γ BHC dust, respectively. Apart from the varietal and treatment differences, the main difference between the two experiments was that the Zanzibar cashew suffered from severe water-logging at the beginning of the season and in consequence had a delayed, but shortened, growth period which prevented the build-up of large *Helopeltis* populations. The Mozambique cashew, being on a well-drained site, had a normal growth period and was heavily attacked by *Helopeltis*. Considerable cross-infestation occurred from untreated to treated plots and from the adjacent

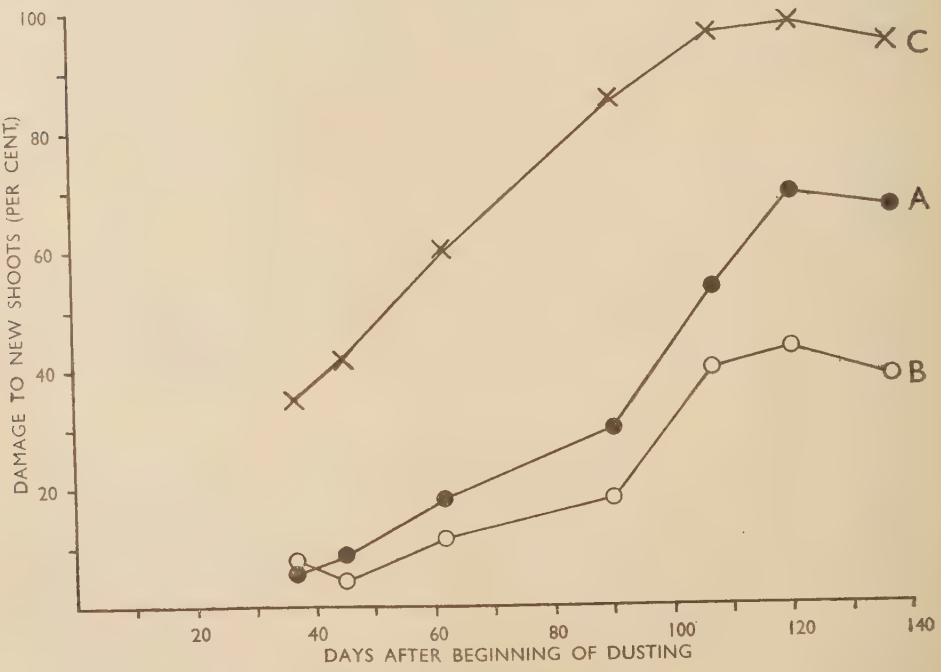


Fig. 1.—Effect of dusting with 0·5 per cent. γ BHC dust in preventing *Helopeltis* damage to shoots of 2-yr.-old Mozambique cashew. Chambezi, Bagamoyo, 1955. A, 5 applications; B, 8 applications; C, control, untreated.

undusted six-acre block in the experiment with the Mozambique cashew, and this may have reduced the effectiveness of the treatments. Nevertheless some indication of the effect of *Helopeltis* is apparent in the results.

Damage was assessed at different times and by more than one method. Early in the growing season, 15 green terminal shoots on each of five trees in a row down the middle of each of the blocks were examined and scored clean = 0, light = 1, moderate = 2, and heavy = 3. Damage to the same number of flowering shoots was assessed by the same method on the same trees, and also by the percentage of these shoots that bore open flowers. Later, counts

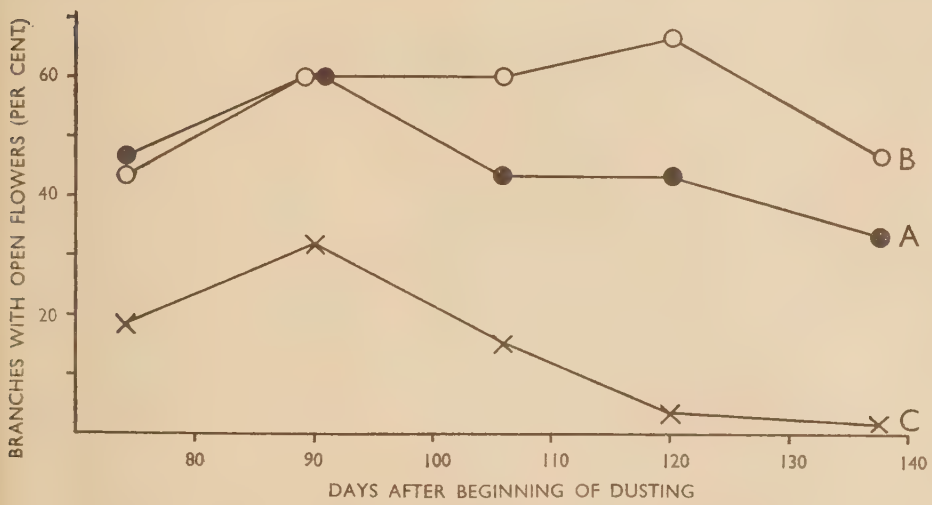


Fig. 2.—Effect of *Helopeltis* on flower production in 2-yr.-old Mozambique cashew. Chambezi, Bagamoyo, 1955. A, 5 applications of 0·5 per cent. γ BHC dust; B, 8 applications of γ BHC dust; C, control, untreated.

were made on the same trees of the percentage of the same number of shoots that bore nuts. The yield of nuts from the treated and untreated plots was also recorded. The protection afforded by dusting the Mozambique cashew with a 0·5 per cent. γ BHC dust is shown in fig. 1 by comparison of the percentage damage to treated and untreated new shoots, whilst the increase in percentage

TABLE III.

Effect of dusting with 0·5 per cent. γ BHC dust against *Helopeltis* spp. on 2-yr.-old cashew, variety Mozambique. Chambezi, 1955.

No. of applications and cost	Flowering shoots bearing nuts 120 days after beginning of dusting (%)	Crop yield (kg./acre)	Loss per acre based on price of nuts Shs. 1/- per kg. (Shs.)
—	0·7	9·7	—
5 (Shs. 33/-) ..	17·3	19·5	23/20
8 (Shs. 52/80) ..	44·7	48·9	13/60

TABLE IV.

Effect of dusting with 5 per cent. DDT and 0·5 per cent. γ BHC dust against *Helopeltis* spp. on 2-yr.-old cashew, variety Zanzibar. Chambezi, 1955.

Treatment	No. of applications and cost per acre	* Percentage damage to flowering shoots 79 days after beginning of dusting	Flowering shoots bearing nuts 79 days after beginning of dusting (%)	Crop yield (kg./acre)	Loss per acre based on price of nuts Shs. 1/- per kg. (Shs.)
Control	—	80·4	40·0	51·5	—
5% DDT dust	14 (Shs. 173/50)	5·3	45·3	87·3	137/70
0·5% γ BHC dust ..	14 (Shs. 92/40)	9·0	37·3	88·1	55/80

* Based on damage scored, clean = 0, light = 1, moderate = 2, heavy = 3.

of branches with open flowers on treated trees is shown in fig. 2. In the Zanzibar cashew the effect of dusting in increasing the yield was not so marked as the infestation was smaller. The count of shoots bearing flowers in this variety on 12.x.55 (65 days after the beginning of dusting) showed that 62·6 per cent. of terminals bore flowers in the untreated controls compared with 98·6 per cent. in both the DDT and BHC plots.

The percentage of flowering branches bearing nuts, and the yields for the two experiments, are given in Tables III and IV. Whilst dusting increased the amount of crop, in neither case did it prove an economic increase. This was the first year of bearing, however, and therefore only relatively small basic yields could be expected.

In the Zanzibar cashew treated with 5 per cent. DDT dust, heavy infestations of unidentified species of *Pseudococcus* and *Ceroplastes* developed towards the end of the season. No abnormal outbreaks of these insects appeared in the cashew treated with the 0·5 per cent. γ BHC dust.

Practical Control Measures.

Factors which have to be taken into account when considering practical insecticide control measures against *Helopeltis* on cashew are the physical difficulty of applying insecticide to full-grown cashew trees, which may reach a height of 25–30 ft. and be 40–50 ft. in diameter, the scattered nature of the planting in peasant agriculture and the difficulty of obtaining adequate supplies of water for spraying. Trials to date have been carried out with dusting, rather than spraying, machines, and considerable promise has been shown by the Swiss-made Mistral I knapsack-type power duster. During 1956, all the three-year-old cashew at Chambezi, Bagamoyo, which had been previously heavily infested in 1955, was dusted with 0·5 per cent. γ BHC dust using the Mistral duster. Three applications, commencing 26.vi.56, were made at intervals of 15 days, 30 lb. of dust being used per acre at each application. No records of damage caused by *Helopeltis* during the season are available owing to the absence of the writer on vacation leave. The Agricultural Officer at Chambezi reported, however, that *Helopeltis* and its damage were difficult to find after the dusting was complete and the trees remained practically free up to the time of my last visit on 15.viii.57. Undusted African-owned trees of about the same age, 170–400 yards away from the Mozambique cashew, and Government-owned two-year-old cashew trees 200 yards away were quite obviously damaged by *Helopeltis* when seen on 15.iv.57 and again on 28.vi.57, 17.vii.57 and on 15.viii.57. On this last date, scores of damage to new branches were: 4-yr. Mozambique cashew, 3·5 per cent. (525 branches), 4-yr. Zanzibar cashew, 0·3 per cent. (256 branches), 4-yr. African-owned cashew, 15·3 per cent. (90 branches), 2-yr. Government cashew, 23·0 per cent. (255 branches).

During 1957, dusting trials proposed for the four-year-old cashew at Chambezi were not carried out as insufficient infestation existed. Dustings were done instead at Morogoro, in Eastern Province, all applications being made with the Mistral duster. Three experiments were carried out, in which the percentage damage on treated and control trees was assessed by examination of branches and the allocation of scores, as described on p. 175. In the first experiment, an isolated, mature tree, 20–25 ft. in height and 45 ft. in diameter, was dusted with 3 lb. of a 0·5 per cent. γ BHC dust, three times, beginning 26.vii.57 and with intervals of 15 and 14 days between dustings. This tree had been heavily damaged by *Helopeltis* every year since the writer first saw it in 1953. Another isolated, mature tree, also with a known record of heavy damage, was selected as control. Adults of *Helopeltis* sp. were seen on both trees on 11.vii.57, when fresh damage was in evidence. On 8.viii.57, 13 days after the first dusting, 11

TABLE V.

Effect of dusting with 0·5 per cent. γ BHC dust against *Helopeltis* on cashew. Morogoro, 1957.

Date	Expt. 1 Single (mature) trees			Expt. 2 20 trees (2–3 yr. old) very heavily attacked		Expt. 3 56 trees (3–4 yr. old)		
	No. of branches examined	Damage (%)		No. of branches examined	Damage (%)	No. of branches examined	Damage (%)	
		Dusted	Undusted		Dusted		Dusted	Undusted
15.ix.54 ..	250	64·0	17·7	—	—	—	—	—
10.iv.56 ..	100	34·0	18·0	—	—	—	—	—
2.vii.57 ..	15	2·2	0·0	—	—	—	—	—
12.viii.57 ..	50	5·3	11·3	—	—	105	6·4	10·6
22.viii.57 ..	100	8·0	31·0	—	—	—	—	—
26.viii.57 ..	100	5·3	27·6	—	—	105	4·8	14·7
5.ix.57 ..	100	2·7	42·4	45	5·8	105	7·4	31·4
16.ix.57 ..	100	4·3	48·3	45	5·7	—	—	—

Insecticide applied to all experiments on 26.vii.57, 10.viii.57, 24.viii.57 and, in addition, on 7.ix.57 to Experiments 2 and 3.

adults of *Helopeltis* sp. were counted after 15 minutes' search on the control; none was found on the dusted tree. The only nymphs found on the dusted tree, seven in total, were in the second and third stages. In the second experiment, a group of 20 trees, two to three years old, whose growth had been completely stopped by *Helopeltis*, were given four applications of 5 lb. of a 0·5 per cent. γ BHC dust on 26.vii.57, 10.viii.57, 24.viii.57 and 7.ix.57. At the beginning of the dustings, adults of *Helopeltis* sp. rose in clouds as the dust spread through the trees, but no adults and no nymphs were found at the end of the dustings, even after prolonged search. With the reduction of the *Helopeltis* population, new growth, almost free of damage, began to appear on the trees towards the middle of August. Damage counts made on 5.ix.57 and 16.ix.57 gave figures of 5·8 and 5·7 per cent., respectively. There were no control trees in this experiment. In a third experiment, two rows of trees, 3–4 years old, 56 in number, were dusted four times (on same dates as Expt. 2) with 11 lb. of a 0·5 per cent. γ BHC dust and two rows of trees of the same age, 50 yards away, were used as control. Some cross-infestation by adult bugs took place from the controls to the treated trees in Experiment 3, but the effect of dusting in reducing damage in this experiment, as in Experiment 1, could be clearly seen. The records of the Morogoro dustings are given in Table V. Unfortunately, observations could not be carried out to harvest time as the writer was transferred from Morogoro in the middle of September, but even at that time obvious increases could be seen in the amount of crop forming on the dusted trees as compared with the undusted trees in Experiments 1 and 3.

Discussion.

Whilst there is sufficient evidence to show that *Helopeltis* spp. can cause serious damage to cashew, considerably more information is required on the status of these pests under conditions of peasant agriculture. Apart from the direct losses of crop caused in any one year, *Helopeltis* is responsible for a general retardation in the growth of the tree, which is reflected in decrease in crop in future years. In a young tree, the onset of cropping, which normally occurs in the second year, may be delayed for a number of seasons. One-year-old trees are not usually attacked by *Helopeltis*. A two-year-old tree has only a small number of shoots but these are very succulent and ideal for the feeding and multiplication of *Helopeltis*, and damage is correspondingly severe. Heavy damage in these early stages causes severe stunting of the tree, as witnessed at Chambezi, in September 1957, where a four-year-old tree, known to have been heavily attacked in its second and subsequent years, was only four ft. tall compared with nearby four-year-old trees, which had not been heavily damaged, and which were between 15 ft. and 20 ft. in height.

Further work is needed on methods of control suited to the crop and to the areas and conditions under which it is grown. At the coast in the Southern Province the main growth of the tree begins in late May or early June with the formation of vegetative shoots. Open flowers begin to appear 5 to 6 weeks later, the flowering period extending for a further two months to early September. In the coastal areas of the more northerly Eastern Province, and in the higher areas inland from the coast, these events are correspondingly later, presumably due to seasonal and temperature effects. At Chambezi in the Eastern Province, in 1955, the main growth of the Mozambique cashew began in the middle of June. Flowering began about 45 days later, at the end of July, and extended almost to the end of September. In the experiments at Morogoro, which is 120 miles from the coast and at an altitude of 2,000 ft., flowering in Experiment 1 did not begin until after the third dusting was completed on 24.viii.57, whilst flowering on the trees in Experiment 3 did not begin until after the fourth dusting on 7.ix.57. These latter trees were growing under somewhat unfavourable

conditions on the lower slopes of the Uluguru Mountains at Morogoro at an altitude of about 2,500 ft. above sea-level.

To prevent undue reduction of pollinating insects (mostly MELIPONIDAE, but some APIDAE), it would seem advisable not to apply insecticide during flowering, but to carry out control measures before the onset of flowering and, if required, after flowering. At Chambezi in 1955 it had originally been intended not to apply insecticide during the flowering period of the Mozambique cashew, but owing to the small size of the plots heavy cross-infestation by adult *Helopeltis* took place from the untreated trees necessitating a change of plan. In the blocks where five applications of insecticide were made, three of these were given before flowering began, the fourth was given during the middle of the flowering period in August and the final one when flowering was complete. In the blocks receiving eight applications of insecticide, four of these were made before flowering, two during flowering and two after flowering. During 1956 at Chambezi, where the possibility of cross-infestation was eliminated by treating all the cashew, and in the experiments at Morogoro, indications of a successful control were obtained from dustings carried out before flowering only. An interval of 15 days between applications was decided upon in these latter experiments as the egg stage, which is unaffected by BHC and DDT, lasts approximately 15 days. The first-stage nymphs emerging after that time are readily killed by these insecticides.

No work has been done on the suitability of low-volume insecticide spraying against *Helopeltis* on cashew owing to lack of suitable equipment. Efficient knapsack-type power sprayers are, however, now available and these should be tested under local conditions. The success of low-volume applications of γ BHC sprays against Mirid bugs on mature cacao trees in Ghana (Crowdy & Elias, 1956) points strongly to the possibility of success of a similar technique against *Helopeltis* spp. on cashew.

Summary.

Cashew, *Anacardium occidentale*, an increasingly important cash crop in the coastal region of Tanganyika, is damaged by two widely distributed species of *Helopeltis*, *H. anacardii* Miller and *Helopeltis* sp.

At Bagamoyo, in June 1955, the period from egg to adult for *H. anacardii* occupied 35·9 days; that for *Helopeltis* sp. occupied 39·2 days.

Damage is caused to the leaves, shoots, buds, young fruits and to the cashew apple. Damage in a young tree is more marked than that in an old tree and may result in its being malformed or stunted.

The build-up of *Helopeltis* populations on cashew follows the main growth period of the crop which begins shortly after the end of the main rains in May. The insects are readily found from July to October–November, when the crop matures.

Application of a 0·5 per cent. γ BHC dust and a 5 per cent. DDT dust to two-year-old trees increased the amount of crop but the increase was not economic owing to the fact that the trees were coming into bearing for the first time. Cross-infestation from untreated plots may also have reduced the effectiveness of the treatments.

Three or four applications by a knapsack-type power duster of 0·5 per cent. γ BHC dust at 15-day intervals previous to flowering of the main crop gave promise of successful control in the field.

References.

CROWDY, S. H. & ELIAS, R. S. (1956). Cacao diseases.—*Outlook on Agric.* **1** no. 2 pp. 64–69.

GOLDING, F. D. (1945). Notes on *Helopeltis sanguineus*, Popp., on cotton in Nigeria.—*Bull. ent. Res.* **36** pp. 75–78.

KIRKPATRICK, T. W. (1941). *Helopeltis* (Hem. Capsidae) on cinchona.—*Bull. ent. Res.* **32** pp. 103–110.

MILLER, N. C. E. (1954). Two new species of Miridae (Hemiptera-Heteroptera). —*Bull. ent. Res.* **45** pp. 703–705.

PATTERSON, W. H. (1914). Report of the Entomologist.—*Rep. agric. Dep. Gold Cst 1913* pp. 18–27.

SWAINE, G. (1956). Annual report of the Entomologist, Morogoro, for the year 1955.—*Rep. Dep. Agric. Tanganyika 1955* pt. 2 pp. 38–42.

© Commonwealth Agricultural Bureaux, 1959.



FIG. 1. Cashew stem and leaves damaged by *Helopeltis*. Bagamoyo, June 1955.



FIG. 2. Malformation of 2-year-old cashew tree caused by *Helopeltis*. Bagamoyo, June 1955.



FIG. 3. *Helopeltis* damage to developing cashew fruit, Bagamoyo, June 1955.

INFECTIBILITY OF TSETSE FLIES, *GLOSSINA PALPALIS* (R.-D.) AND *G. TACHINOIDES* WESTW. WITH *TRYPANOSOMA VIVAX*.

By F. A. Squire *

Senior Entomologist, Department of Agricultural Research, Ibadan, Nigeria.

The following observations were made at Dorimon (lat. 10°1′N. long. 2°40′W.), in the extreme north-west of Ghana, during the hot months of March and April in 1954. The flies used in this investigation emerged in the laboratory from pupae collected along the banks of the Black Volta six miles away to the west. The adults were kept singly in open-ended glass tubes (6″ × 1″), plugged at one end with cotton-wool and covered at the other with mosquito netting, the tubes being kept sloping in a shallow dish with the cotton-wool end making contact with water and the other end resting on the edge of the dish. None of the flies had mated.

In connection with the theory put forward by Burtt (1946) concerning the subsequent effect on adult infectibility of the prevailing temperature during the pupal phase of the fly, it should be stated that the shade temperature along the banks of the Black Volta during the period when the pupae were collected ranged from 70 to 98°F.

The flies were fed on West African dwarf forest goats derived from the nearby village of Pesa, which were either naturally infected or artificially infected by syringe from goats infected with *Trypanosoma vivax*. The flies were fed on those goats actually showing numerous trypanosomes in the blood at the time of feeding as determined by wet smears; the temperature of the laboratory ranged between 85 and 95°F. and the relative humidity from 60 to 80 per cent. at the time of feeding, and the body temperature of the goats ranged from 102 to 104°F. Thus the temperature first encountered by the trypanosome in its new host, the fly, was at the outset never more than 19°F. lower than that in its previous host, the goat.

Some of the flies, after they had taken several infective meals, were fed at times on infected goats in the negative phase, *i.e.*, not showing trypanosomes in the blood at the time of feeding though known to be infected, and at other times on a spurwing goose (*Plectropterus gambensis*), the idea being to see whether a meal from a susceptible host in the negative phase or from a refractory host of a different class would interrupt infection in view of the *in vitro* findings of Adams (1931) on *T. rhodesiense* and *T. gambiense* from the mid-gut and salivary glands of *Glossina palpalis* (R.-D.).

Results and Discussion.

The results are set forth in Tables I and II and are summarised in Tables III and IV. The rate of infection in young flies less than 14 days old is given in Table V. Table III takes into account infections in both or either the labrum and hypopharynx. In other words it counts young colonies in the labrum which have not given rise to metacyclic forms in the hypopharynx, as well as those

* Formerly Director of Tsetse Control, Ghana.

which had already given rise to such forms and in addition those cases in which the original labrum infection had been lost leaving only the mature forms in the hypopharynx. It will be seen that on this score 56·1 per cent. of the flies were infected. Applying the χ^2 test with the correction for continuity there is no significant difference between the infection rates in the different categories. But

TABLE I.

Records of infection in individual examples of *G. palpalis*.

Number of fly	Age in days when dissected	Feeding history : number of times fed on positive goat (p), negative goat (n) and spurwing goose (s)	Labrum	Hypopharynx
		Males		
5	13	4p, 1s, 4p, 1s	—	—
13	16	8p, 1s, 4p	—	+
16	12	6p, 1s, 2p, 1s	+	+
17	13	9p	—	+
18	10	6p	—	+
20	13	10p	—	+
29	12	7p	—	+
40	11	8p	—	—
44	13	6p	—	—
47	12	7p, 1n	+	+
54	13	7p	+	+
56	11	6p	—	+
59	11	7p	D	+
62	13	9p, 1n	+	+
69	9	7p, 1n	—	+
70	10	5p	—	—
71	9	8p	—	—
72	7	6p	+	—
		Females		
5	38	10p, 20s	—	—
6	38	6p, 25s	—	—
7	16	8p, 1s, 4p	—	—
11	10	4p, 1s, 2p	—	—
14	10	5p, 1s, 2p	—	—
23	13	4p, 1s, 2p	+	—
27	11	5p	—	—
31	11	6p	—	+
34	10	6p	—	—
37	10	7p	—	—
43	14	11p	—	—
49	10	7p	—	—
50	14	7p, 1n	—	+
52	19	13p, 1n	D	+
54	27	23p, 1s, 1n	+	+
55	14	10p, 1n	—	—
56	28	21p, 2s	—	—
59	25	18p, 2s	—	—
61	10	7p	—	+
66	9	5p, 1n	—	+
69	22	13p	—	—
73	10	9p	+	+
74	9	7p	+	+
75	9	8p	—	—
76	9	7p	—	—
77	9	9p	—	—

D. Dead colony.

Records of infection in individual examples of *G. tachinoides*.

Number of fly	Age in days when dissected	Feeding history : number of times fed on positive goat (p), negative goat (n) and spurwing goose (s)	Labrum	Hypopharynx
		Males		
12	16	9p, 1s, 2p	+	—
14	41	7p, 25s, 1p	—	—
34	40	7p, 27s, 2p	—	—
39	14	11p	—	—
41	10	10p	+	—
57	14	10p, 1n	+	—
58	13	11p	+	+
60	13	11p	+	+
64	24	16p	+	+
65	9	6p	—	—
68	23	16p, 2s	+	—
70	11	10p, 1n	—	—
78	10	10p	+	+
79	10	9p	+	+
80	14	1p, 11s	—	—
81	12	11p	YC +	—
82	11	10p	YC +	—
83	12	11p	+	—
84	9	9p	YC +	—
		Females		
3	36	4p, 24s	—	—
4	41	11p, 23s, 1p	—	—
4	12	5p, 1s, 3p	+	—
5	38	10p, 20s	—	—
6	13	6p, 1s, 4p	+	+
10	15	8p, 1s, 3p	—	+
11	31	8p, 19s, 1p	—	—
18	31	25p, 2s	—	—
19	14	10p, 1s, 2p	—	—
22	20	19p	+	+
23	30	28p, 2s	—	—
25	17	15p	—	—
26	14	8p, 1s, 2p	—	+
27	42	10p, 26s, 2p	—	—
28	45	10p, 24s, 2p	—	—
28 (a)	11	7p	—	—
30	15	12p	—	—
31	37	23p, 12s, 1p	—	+
32	11	7p, 1n	D —	+
38	40	9p, 27s, 2p	—	—
38 (a)	12	9p, 1s	—	—
40	34	25p	—	—
44	31	27p, 2s, 2p	+	+
45	12	10p, 1s	—	+
46	30	25p, 3s, 1p	D —	+
48	28	24p, 1s	+	+
51	12	9p, 1n	—	+
52	26	23p, 1s	—	—
62	23	20p, 2s	+	—
65	22	21p	+	+
67	8	7p	+	—
85	9	9p	+	+
86	10	9p	+	—
87	8	8p	+	—
88	16	15p	+	—
89	14	13p	—	—
90	12	11p	+	+
91	10	9p	—	—
92	10	9p	+	+
93	10	8p	—	—
94	9	8p	YC +	—
95	8	7p	+	+
96	12	11p	YC +	—
97	8	6p	YC +	—

D. Dead colony. YC. Young colony.

if females of *G. palpalis* are compared with the other three groups together it shows a significantly lower infectibility at the 0·05 level. Table IV summarises the number of flies with the labrum infected. It includes those with the hypopharynx positive as well but excludes those which have only the hypopharynx infected, *i.e.*, those that have lost their labrum infection. Here the total rate of infection is only 37·4 per cent. and the difference is due to the heavy loss of labrum infection in both sexes of *G. palpalis* and to a lesser extent in the females of *G. tachinoides* Westw. There is a significant difference at the 0·01 level between *G. palpalis vs. G. tachinoides* taking the sexes together and at the 0·05 level between the males of the two species. In both cases, *G. tachinoides* appears the more infectible. Since the trypanosomes first colonise and multiply in the labrum, the mature forms passing thence to the hypopharynx, it follows that flies with the hypopharynx positive and labrum negative must at one time have had the labrum positive as well. So the loss of infection can be expressed as:—

$$\frac{\text{Flies with hypopharynx positive and labrum negative} \times 100}{\text{Flies with hypopharynx positive}}$$

From Tables I and II it will be seen that the loss of labrum infection is as follows:—

		HP+LN	HP	$\frac{HP+LN \times 100}{HP}$
G. palpalis	Male	8	12	66·7
	Female	5	8	62·5
G. tachinoides	Male	0	5	–
	Female	7	16	43·8
		20	41	
		General rate 48·8%.		
G. palpalis	M+F	13	20	65
G. tachinoides	M+F	7	21	33·3

G. tachinoides appears therefore to be more tenacious of infection than *G. palpalis*.

There is evidence that loss of infection can take place quite early. Thus, considering flies less than 14 days old, the loss amounted to 46·4 per cent. The

TABLE III.

Trypanosomes in labrum and (or) hypopharynx (summarised from Tables I & II).

G. palpalis				*G. tachinoides*			
	Infected	Not infected	Totals		Infected	Not infected	Totals
Males	13	5	18	Males	13	6	19
Females	9	17	26	Females	25	19	44
Totals	22	22	44	Totals	38	25	63

Percent. infected :

Males : 72·2
Females : 34·6

Males : 68·4
Females : 56·8

General rate : 56·1

earliest losses recorded were in *G. palpalis*: male No. 69 and female No. 66, both by the ninth day after emergence.

The rate of infection in young flies is treated separately in Table V. It will be seen that the general rate, 67·8 per cent., is higher than that of Table III, from which it may be concluded that there is, on balance, a loss rather than a gain in the rate of infection as the fly population ages. This is in agreement (not taking loss of infection into account) with the findings of Duke (1935) that repeated infective meals only slightly increase the rate of infection. But it does not accord with Squire (1951) who found that wild examples of *G. palpalis* in Sierra Leone showed higher infection rates in the older age-groups. But it must be remembered that the laboratory flies were fed on highly infective material whereas the wild flies had to take their chance on picking up an infection. It is also possible that flies constantly exposed to infection acquire an immunity, which would be less likely to happen to wild flies. There is no significant difference between the categories, but females of *G. palpalis vs.* the other three groups together gives a difference significant at the 0·05 level.

TABLE IV.

Trypanosomes in labrum and labrum & hypopharynx
(summarised from Tables I & II).

G. palpalis				*G. tachinoides*			
	Infected	Not infected	Totals		Infected	Not infected	Totals
Males	5	13	18	Males	13	6	19
Females	4	22	26	Females	18	26	44
Totals	9	35	44	Totals	31	32	63

Percent. infected :

Males :	27·8	Males :	68·4
Females :	15·4	Females :	40·9

General rate : 37·4

The earliest case of hypopharynx infection observed was in female No. 95 of *G. tachinoides*, eight days after emergence. Assuming that this figure represents the minimum maturation period under these conditions and assuming also that there was no earlier infection which had died out completely in both labrum and hypopharynx, it is possible to estimate approximately the earliest possible date of infection in those flies with only the labrum infected by counting eight days back from the date of dissection, the argument being that had they been infected earlier the trypanosomes would have appeared in the hypopharynx. On this basis, female No. 23 of *G. palpalis* became infected not before the fifth day, female No. 88 of *G. tachinoides* not before the eighth day and male No. 68 of *G. tachinoides* not before the 15th day. Thus there is evidence, though not conclusive, that later infections do occur, though early infection appears to be the rule. Young colonies of only a few trypanosomes to the cluster were seen in six cases, all less than 13 days old. The absence of such colonies from older flies again suggests that later infections are comparatively rare.

Some flies appear to be uninfectible, thus male No. 44 of *G. palpalis* after 13 days, female No. 69 after 22 days and female No. 40 of *G. tachinoides* after

34 days. These all fed exclusively on goats showing numerous trypanosomes in the peripheral blood-stream at the time of each feed. Altogether, out of 107 flies, 47 remained uninfected in spite of having had on the average 10·6 infective meals per fly.

Taylor (1932) found that by raising the temperature of the imago to 37°C. (98°F.) for considerable periods during the first four days of infection, the infection rate rose to 75 per cent. The laboratory temperatures at Dorimon approximate to this and so do some of the infection rates.

TABLE V.

Infection rates in young flies, less than 14 days old (labrum and (or) hypopharynx) (summarised from Tables I & II).

G. palpalis				*G. tachinoides*			
	Infected	Not infected	Totals		Infected	Not infected	Totals
Males	12	5	17	Males	9	2	11
Females	6	9	15	Feamles	15	4	19
Totals	18	14	32	Totals	24	6	30

Percent. infected :

Males : 70·6
Females : 40·0

Males : 81·8
Females : 78·9

General rate : 67·8

Desowitz & Fairbairn (1955) found that raising the temperature of the infected fly shortens the developmental cycle of the trypanosome. In some of their observations, *T.. vivax* became metacyclic in five days in flies kept at 29°C. (84·2°F.). Laboratory temperature at Dorimon was not controlled, but rose above 100°F. in the afternoon and fell to 70°F. at night. Here the shortest maturation period observed was eight days. The optimum temperature for infection to take place is not known, but it is suggested that it may be related among other things to the normal body temperature of the mammalian donor host. Tenacity of infection may depend on atmospheric humidity in the case of *T. vivax* owing to its comparatively exposed anatomical location in the labrum.

Some of the flies which had received several infective meals were fed, 24 hours prior to dissection, on goats in the negative phase of infection and (or) on a spur-wing goose in order to see whether these sera would prove hostile to infection. As far as could be seen from the infected flies the trypanosome colonies seemed to be undisturbed by the change of diet.

Summary.

Observations were made at Dorimon in the extreme north-west of Ghana, during the hot months of March and April 1954, of the infectibility of *Glossina palpalis* (R.-D.) and *G. tachinoides* Westw. with *Trypanosoma vivax*.

Pupae were obtained from the Black Volta where shade temperatures ranged from 70 to 98°F. and the flies that emerged from them were kept singly in small glass tubes in the laboratory at a temperature of 85 to 95°F. and a relative humidity of 60 to 80 per cent. They were given several feeds on infected goats. The following percentage rates of infection were observed.

Labrum and (or) hypopharynx: General rate, 56·1; males of *G. palpalis*, 72·2, females, 34·6; males of *G. tachinoides*, 68·4, females, 56·8.

Labrum only and labrum & hypopharynx: General rate, 37·4; males of *G. palpalis*, 27·8, females, 15·4; males of *G. tachinoides*, 68·4, females, 40·9.

Early infection is the rule but late infections occurred. Some flies appear to be uninfectible. Thus, out of 107 flies, 47 remained uninfected in spite of having had on the average 10·6 infective meals per fly. A high percentage of flies lost their labrum infection.

The following percentage loss of labrum infection was recorded: General rate, 48·8; males of *G. palpalis*, 66·7, females, 62·5; males of *G. tachinoides*, nil, females, 43·8.

G. tachinoides appears to be more tenacious of infection than *G. palpalis*. Feeding infected flies on goats in the negative phase and (or) on spurwing goose (*Plectropterus gambensis*) did not appear to have any adverse effect on the colonies of trypanosomes in the labrum.

References.

Adams, A. R. D. (1931). The action of various sera, *in vitro*, on the gut and salivary gland forms of *T. rhodesiense* and *T. gambiense* from *Glossina palpalis*.—*Ann. trop. Med. Parasit.* **25** pp. 299–311.

Burtt, E. (1946). Incubation of tsetse-flies: increased transmission-rate of *Trypanosoma rhodesiense* in *Glossina morsitans*.—*Ann. trop. Med. Parasit.* **40** pp. 18–28.

Desowitz, R. S. & Fairbairn, H. (1955). The influence of temperature on the length of the developmental cycle of *Trypanosoma vivax* in *Glossina palpalis*.—*Ann. trop. Med. Parasit.* **49** pp. 161–163.

Duke, H. L. (1935). Studies on the factors that may influence the transmission of the polymorphic trypanosomes by tsetse. IX. On the infectivity to *Glossina* of the trypanosome in the blood of the mammal.—*Ann. trop. Med. Parasit.* **29** pp. 131–143.

Squire, F. A. (1951). Seasonal variation in the incidence of *Trypanosoma vivax* in *Glossina palpalis* (R.-D.).—*Bull. ent. Res.* **42** pp. 371–374.

Taylor, A. W. (1932). The development of West African strains of *Trypanosoma gambiense* in *Glossina tachinoides* under normal laboratory conditions, and at raised temperatures.—*Parasitology* **24** pp. 401–418.

© Commonwealth Agricultural Bureaux, 1959.

OBSERVATIONS ON THE MOSQUITO FAUNA OF MOMBASA.

By C. Teesdale

Division of Insect-borne Diseases, Nairobi, Kenya.

The following observations were made on Mombasa Island and the adjacent mainland at various times between 1943 and 1951. It is hoped that they will serve to supplement recent work on the mosquitos of the Kenya coast, much of which was done at Ganda and Mambrui about 70 miles farther north (van Someren, Heisch & Furlong, 1958). The climate and geographical features of the Mombasa area have already been described in detail by Teesdale (1955).

Methods.

Four catching methods were used in obtaining data, on Mombasa Island between 1943 and 1944, and on the mainland between 1949 and 1952: (1) day-time catches with hand nets in the bush, (2) window-trap catches, (3) diurnal biting catches in the bush and (4) twenty-four hour biting catches in different situations. All biting catches were on human bait and the 24-hour catches were personally supervised by the writer. Trained African entomological staff was used throughout the observations. The different methods are now described in more detail.

*1. Day-time net catches in bush.**

Net catches in bush were made by teams of Africans consisting of three to nine men using small hand nets to capture mosquitos in various ways. Thus, sometimes the catchers sat in different places in the bush for periods of about 15 minutes; at other times some remained at the same site throughout the catching period, while others walked slowly through the bush.

Catches usually started at 07 hr. (occasionally at 06 hr.) and ended at 18 hr. (East African Standard Time), the teams working on a three-hour shift.

The methods gave rather different results. Thus more mosquitos were captured when the team kept moving, while those taken during sitting catches were often unfed females only.

A " catching index ", which gives a rather better basis for comparison than the actual numbers captured, was obtained by dividing the number of each species caught monthly by the total boy-hours spent on the catches. The species taken in these catches are listed in Tables I and II and include all those known to occur in the Mombasa district. Full specific names are given in these Tables but abbreviations are used in the text. With the exception of *Culex horridus*, there was always a preponderance of females in the common species.

2. Window-trap catches.

The traps used were those described by Teesdale (1955) and van Someren, Heisch & Furlong (1958). They were fitted to the windows of huts in the village of Jomvu Kuu about 8 miles west of Mombasa. Each window served one room only, and all rooms had ceilings which prevented the passage of mosquitos into and out of the rooms by the roof and its eaves. From January 1950 to July 1951

* Bush is used as a general term to describe any situation not actually in a village compound; it may include native cultivation, coconut plantations and open grassy patches as well as low-growing indigenous bush.

TABLE I.

Net catches in bush (Mombasa, 1943 and 1944; Kwa Shekh, 1950 and 1951). Common species.

Month	*Aëdes* (*Stegomyia*) *aegypti* (L.)		*Aë.* (*S.*) *simpsoni* (Theo.)		*Aë.* (*S.*) *metallicus* (Edw.)		*Aë.* (*Aëdimorphus*) *albocephalus* (Theo.)		*Aë.* (*Skusea*) *pembaensis* (Theo.)		*Aë.* (*Bunksinella*) *albicosta* (Edw.)		*Culex* (*Culex*) *pipiens fatigans* Wied.		*C.* (*Culex*) *duttoni* Theo.		*C.* (*Culiciomyia*) *nebulosus* Theo.		*C.* (*Neoculex*) *horridus* Edw.		*C.* (*Lutzia*) *tigripes* Grp.		*Eretmapodites subsimplicipes* Edw.		*E. quinquevittatus* Theo.	
	Msq.	Index	Msq.	Index	Msq.	Index	Msq.	Index	Msq.	Index	Msq.	Index	Msq.	Index	Msq.	Index	Msq.	Index	Msq.	Index	Msq.	Index	Msq.	Index	Msq.	Index
Jan.	355	0·5	23	0·04	27	0·04	24	0·04	1032	1·6	1728	2·7	467	0·7	6	0·01	74	0·12	17	0·03	3	—	89	0·14	15	0·02
Feb.	413	0·8	7	0·01	1	—	31	0·05	601	0·9	753	1·2	438	0·7	1	—	19	0·03	P	—	12	0·02	21	0·03	2	—
Mar.	128	0·2	75	0·1	17	0·03	60	0·09	669	1·0	547	0·8	905	1·4	3	—	P	—	4	—	13	0·02	49	0·07	1	—
Apr.	138	0·3	166	0·3	37	0·09	67	0·1	588	1·2	817	1·7	1166	2·3	105	0·2	7	0·02	36	0·09	23	0·05	81	0·16	50	0·10
May	784	1·3	421	0·7	77	0·1	178	0·3	589	0·9	780	1·25	1663	2·7	24	0·04	0	—	14	0·02	407	0·65	59	0·09	10	0·02
June	1304	2·4	248	0·5	78	0·1	162	0·3	282	0·5	62	0·3	2629	4·8	84	0·16	P	—	23	0·04	377	0·70	252	0·47	19	0·35
July	559	1·2	96	0·2	38	0·09	35	0·08	818	1·8	167	0·4	1719	3·7	40	0·09	499	1·08	33	0·08	206	0·44	337	0·73	84	0·18
Aug.	886	1·7	138	0·3	22	0·05	28	0·06	898	1·8	51	0·1	1613	3·2	58	0·12	125	0·25	14	0·03	91	0·18	305	0·60	100	0·20
Sept.	970	1·7	492	0·9	0	—	3	0·01	933	1·7	21	0·04	731*	2·3	23*	0·07	148	0·26	9	0·02	6	0·01	69	0·12	109	0·19
Oct.	766	1·3	239	0·4	2	—	19	0·03	1285	2·1	42	0·07	453*	1·4	29*	0·09	69	0·11	1	—	1	—	50	0·08	17	0·03
Nov.	827	1·5	118	0·2	1	—	126	0·2	664	1·2	602	1·1	1609	2·9	58	0·10	53	0·10	21	0·04	29	0·05	66	0·12	10	0·02
Dec.	1537	2·3	148	0·2	2	—	118	0·2	493	0·7	1137	1·7	2372	3·5	86	0·13	279	0·42	22	0·03	179	0·27	90	0·14	15	0·02
Totals	8667		2171		302		851		8852		6707		15765		517		1273		194		1347		1468		432	
Ratio ♂: ♀	4:7		5:16		14:15		3:14		2:7		2:9		3:8		1:6		5:12		3:2		5:7		2:5		2:9	

* Excluding 1944. P = Present in small numbers.

the traps were examined at 07, 12 and 18 hr. Monthly totals of four of the common species, divided into day and night captures, are given in Table III. The latter include all mosquitos entering the traps between 18 and 07 hr. the following morning, and the day captures those between 07 and 18 hr. During daylight, slightly more mosquitos of all species entered between 12 and 18 hr. than between 07 and 12 hr. but the numbers are not worth indicating separately.

TABLE II.

Net catches in bush (Mombasa, 1943 and 1944; Kwa Shekh, 1950 and 1951).
Less common species.

Aëdes (*Aëdimorphus*) *haworthi* Edw.
Aë. (*Aëdimorphus*) *argenteopunctatus* (Theo.)
Aë. (*Aëdimorphus*) *abnormalis* (Theo.) group
Aë. (*Aëdimorphus*) *cumminsi* ssp. *mediopunctatus* (Theo.)
Aë. (*Aëdimorphus*) *tarsalis* (Newst.)
Aë. (*Aëdimorphus*) *tricholabis* Edw.
Aë. (*Banksinella*) *ellinorae* Edw.
Aë. (*Diceromyia*) *adersi* (Edw.)
Aë. (*Finlaya*) *fulgens* (Edw.)
Aë. (*Mucidus*) *scatophagoides* (Theo.)
Aë. (*Stegomyia*) *vittatus* (Big.)
Aë. (*Stegomyia*) *heischi* van Som.
Aë. (*Stegomyia*) *calceatus* Edw.
Anopheles (*Anopheles*) *coustani* Lav.
A. (*Anopheles*) *coustani* var. *ziemanni* Grünb.
A. (*Anopheles*) *coustani* var. *tenebrosus* Dön.
A. (*Anopheles*) *paludis* Theo.
A. (*Myzomyia*) *funestus* Giles
A. (*Myzomyia*) *gambiae* Giles
A. (*Myzomyia*) *pharoensis* Theo.
A. (*Myzomyia*) *squamosus* Theo.
Culex (*Culex*) *poicilipes* (Theo.)
C. (*Culex*) *perfuscus* Edw.
C. (*Culex*) *sitiens* Wied.
C. (*Culex*) *guiarti* Blanch.
C. (*Culex*) *grahami* Theo.
C. (*Culex*) *weschei* ssp. *gediensis* Edw.
C. (*Culex*) *invidiosus* Theo.
C. (*Culex*) *annulioris* Theo.
C. (*Culex*) *decens* Theo.
C. (*Culex*) *tritaeniorhynchus* Giles
C. (*Culex*) *univittatus* Theo.
C. (*Culex*) *simpsoni* Theo.
C. (*Culex*) *antennatus* (Becker)
C. (*Culex*) *trifoliatus* Edw.
C. (*Culex*) *ornatothoracis* Theo.
C. (*Culiciomyia*) *furlongi* van Som.
C. (*Culiciomyia*) *semibrunneus* Edw.
C. (*Culiciomyia*) *cinereus* Theo.
C. (*Neoculex*) *insignis* (Cart.)
C. (*Neoculex*) *wigglesworthi* Edw.
C. (*Neoculex*) *albiventris* Edw.
C. (*Neoculex*) *adersianus* Edw.
Eretmapodites silvestris Ingram & De Meillon
Ficalbia (*Mimomyia*) *splendens* (Theo.)
F. (*Mimomyia*) *mimomyiaformis* (Newst.)
F. (*Mimomyia*) *plumosa* (Theo.)
Toxorhynchites brevipalpis Theo.
Toxorhynchites lutescens Theo.
Taeniorhynchus (*Mansonioides*) *uniformis* (Theo.)
T. (*Mansonioides*) *africanus* (Theo.)
Uranotaenia alboabdominalis Theo.

TABLE III.

Window-trap catches at Jomvu Kuu village, Mombasa, Jan. 1950–July 1951. Day and night captures.

(a) In-going

Species		January		February		March		April		May		June		July		August		September		October		November		December		Totals	
		Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
Aë. aegypti	♂	1	2	0	1	1	2	5	3	9	3	11	5	11	4	1	0	4	3	3	1	2	2	0	4	48	30
	♀	3	4	2	3	0	5	4	8	6	18	14	6	14	10	2	3	10	6	10	5	12	6	4	6	81	80
Aë. pembaensis	♂	0	0	0	0	0	0	1	1	1	1	0	0	1	2	0	0	0	4	0	1	0	0	0	0	3	9
	♀	0	0	1	2	0	3	9	28	7	36	3	4	4	5	0	2	0	3	2	1	0	0	0	0	26	84
C. p. fatigans	♂	3	4	2	0	0	0	6	2	10	4	54	24	15	4	3	2	0	0	1	1	2	0	1	4	97	45
	♀	4	4	2	3	1	1	5	8	11	10	29	22	13	7	1	3	1	3	0	1	1	0	0	3	68	65
A. gambiae	♂	0	0	0	0	0	0	0	0	3	0	12	5	5	2	0	0	0	0	0	0	0	0	0	0	20	7
	♀	0	0	0	0	0	0	0	2	13	6	25	16	5	9	0	2	0	0	0	0	0	0	0	0	43	35

Also recorded : *C. sitiens*, 1 ♀ (day) ; *C. nebulosus*, 1 ♂, 1 ♀ (day), 2 ♂, 3 ♀ (night) ; *A. funestus*, 2 ♂, 3 ♀ (day), 1 ♀ (night).

(b) Out-going

		Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
Aë. aegypti	♂	59	31	82	41	27	36	18	21	50	42	38	25	30	17	36	27	128	62	62	29	122	43	198	87	850	461
	♀	103	89	199	103	78	132	110	137	167	156	114	87	59	74	69	28	129	48	144	60	157	87	302	153	1631	1154
Aë. pembaensis	♂	0	2	1	1	2	8	4	5	8	10	1	10	1	4	1	3	7	15	4	6	1	1	1	2	31	67
	♀	3	40	4	84	8	65	67	188	71	259	6	51	9	24	13	36	4	31	16	44	17	62	11	25	229	909
C. p. fatigans	♂	8	78	7	30	3	8	7	18	106	226	45	136	67	599	2	21	22	65	4	19	7	37	6	66	284	1303
	♀	46	260	28	76	10	23	24	114	117	341	101	478	89	534	7	37	21	61	21	54	19	89	19	170	502	2237
A. gambiae	♂	1	1	0	0	0	0	1	1	3	15	7	15	4	12	0	0	0	0	0	1	0	1	0	1	16	47
	♀	2	2	0	1	0	1	21	42	37	120	131	444	14	55	0	2	0	1	0	0	0	3	6	16	211	687

Also recorded :

Species	Total day and night
C. duttoni	2 ♀
C. decens	14 ♀
C. sitiens	45 ♀
C. cinereus	2 ♀

Species	Total day and night
C horridus	9 ♀
T. africanus	18 ♀
Aë. metallicus	5 ♀
A. funestus	13 ♂ 136 ♀*

* Out of 102 captured at night, 80 were taken in July 1951.

Window-trap captures at Jomvu Kuu village, Mombasa, August–October 1951.

Hourly captures of mosquitos from nine out-going and six in-going traps.

Time (hr.)	In-going								Out-going*							
	C. p. fatigans		*Aë. pembaensis*		*Aë. aegypti*		*A. funestus*		*C. p. fatigans*		*Aë. pembaensis*		*Aë. aegypti*		*A. funestus*	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
07–08	17	14	1	8	5	15	1	9	75	168	1	50	55	130	6	53
08–09	18	17	3	7	15	19	2	5	50	53	3	9	54	94	8	42
09–10	9	15	0	3	16	1	1	6	14	28	0	1	24	42	2	16
10–11	23	13	1	5	30	8	2	7	17	9	1	3	24	35	1	12
11–12	14	5	0	2	17	6	2	4	17	11	0	1	25	12	1	6
12–13	12	3	0	1	16	3	2	3	8	12	0	4	17	20	1	1
13–14	3	6	1	0	9	8	2	1	11	9	0	1	14	27	0	1
14–15	12	3	0	0	7	11	0	0	18	13	1	3	33	48	1	4
15–16	8	4	0	2	2	13	0	1	2	4	0	5	4	86	0	6
16–17	8	1	0	0	4	9	0	1	5	7	1	8	57	109	0	0
17–18	1	6	0	0	6	11	0	0	2	8	1	6	90	154	0	4
18–19	7	8	1	4	1	3	0	1	107	187	2	22	83	163	4	22
19–20	4	3	1	0	0	5	0	2	106	168	3	18	31	52	2	13
20–21	4	2	2	5	3	2	0	0	114	116	9	23	19	30	5	22
21–22	Traps were not examined between these hours								69	18	0	2	0	4	2	2
22–23									28	34	0	4	5	2	1	2
23–00									8	15	0	11	0	1	0	1
00–01									10	8	0	4	2	4	0	4
01–02									5	2	0	2	2	0	1	1
02–03									3	8	0	4	1	1	0	1
03–04									8	13	0	3	2	2	0	5
04–05									9	16	1	4	1	1	1	2
05–06									46	16	1	6	1	1	1	10
06–07									9	16	1	11	7	26	0	5
Totals ..	140	100	10	37	131	114	12	40	741	939	25	205	551	1044	37	235

* N.B.—Out-going captures between 21 and 07 hr. were made once weekly (11 catches), the remainder daily.

TABLE V.

Diurnal biting in bush, Kwa Shekh, June 1949–January 1952. Common species.

	January		February		March		April		May		June		July		August		September		October		November		December		Totals
Boy-hours	128		86		86		60		80		88		78		101		99		116		146		124		
Species	No.	Ind.	No.	Ind.	No.	Ind.	No.	Ind.	No.	Ind.	No.	Ind.	No.	Ind.	No.	Ind.	No.	Ind.	No.	Ind.	No.	Ind.	No.	Ind.	
Aë. simpsoni	230	1·8	3	0·04	0	-	32	0·5	231	2·9	459	5·2	337	4·3	462	4·6	572	5·7	532	4·6	486	3·3	365	2·9	3709
Aë. aegypti	115	0·9	22	0·25	60	0·7	103	1·7	383	4·8	281	3·2	117	1·5	216	2·1	107	1·1	182	1·6	136	0·9	119	0·9	1841
Aë. pembaensis	282	2·2	137	1·8	112	1·3	168	2·8	184	2·3	387	4·4	289	3·7	475	4·7	554	5·6	464	4·0	569	3·9	409	3·3	4030
Aë. metallicus	36	0·3	3	0·03	38	0·4	39	0·7	99	1·2	24	0·3	13	0·2	24	0·2	24	0·2	30	0·3	11	0·08	6	0·05	347
Aë. albicosta	55	0·4	52	0·6	3	0·03	8	0·1	0	-	1	0·01	1	0·01	13	0·1	3	0·03	1	0·01	12	0·08	16	0·1	165
Aë. tricholabis	0		0		0		0		1		3		0		6		0		15		35		9		69
Aë. albocephalus	4		0		0		0		1		2		1		9		4		4		4		1		30
Aë. fulgens	4		0		0		0		1		1		1		0		1		0		1		1		10
C. p. fatigans	1		2		8		1		2		12		7		36		15		42		16		4		146
C. horridus	0		0		0		0		0		0		4		12		2		9		13		5		45
C. sitiens	6		0		2		0		1		0		2		23		25		9		14		7		89
E. quinquevittatus	21		0		0		2		3		8		10		16		14		11		7		12		104
E. subsimplicipes	1		0		0		1		0		1		2		5		5		0		4		0		19

Also recorded : Mombasa and Kwa Shekh

Biting occasionally :
Aë. cumminsi : Jan., Aug., Nov., Dec.
C. invidiosus : Sept., Nov., Dec.
C. weschei var. *mediopunctatus* : July, Aug., Sept.
C. grahami : Jan., Aug., Dec.
C. nebulosus : Jan., Nov., Dec.
C. decens : Apr., May, June, Sept., Oct., Nov.
E. silvestris : Feb., Aug., Sept., Oct., Nov.

Biting rarely :
Aëdes adersi
Aë. tarsalis
Aë. argenteopunctatus
Aë. haworthi
Aë. vittatus
Aë. calceatus
Aë. heischi
Aë. mucidus
Aë. scatophagoides

Taeniorhynchus chrysosoma Edw.
T. africanus
T. uniformis
Uranotaenia alboabdominalis
Aëdomyia furfurea (End.)
Ficalbia plumosa
Anopheles coustani
A. coustani var. *ziemanni*
A. coustani var. *tenebrosus*
A. paludis
A. funestus

A. gambiae
A. pharoensis
A. squamosus
C. cinereus
C. furlongi
C. (*Mochthogenes*) *inconspicuosus* (Theo.)
C. annulioris
C. tritaeniorhynchus
C. univittatus
C. antennatus
C. perfuscus
C. poicilipes

The results of hourly collections from the traps during the three months August to October 1951 are given in Table IV. From 07 to 21 hr. both entry and exit traps were examined daily, but it was not possible to inspect the entry traps at night after the latter hour as they were fixed to the inside of windows in bedrooms. Night-time collections in the exit traps were made once a week; there were always many more out-going than in-going mosquitos. Except for *Aëdes aegypti*, and possibly *Culex pipiens fatigans*, it was almost certain that none of the species was breeding indoors, yet far larger numbers of examples of them were invariably taken in the exit traps. The traps were fitted to windows of rooms with no other access from the outside except through an inner door communicating with the main room of the house. Special care was given in the selection of these rooms to exclude any having spaces between ceilings and walls. It is difficult to find an adequate explanation for the discrepancy between out-going and in-going numbers.

3. Diurnal biting catches in bush.

Biting catches using human bait were either confined to daylight (diurnal) or continued throughout the 24 hours. The former showed which species fed on humans during daylight, and the data obtained were compared with the results of the 24-hour catches. Of the numerous species coming to feed on man in daylight, only 13 did so regularly. They are listed in Table V and a biting index is given for the more important of them.

These day-time biting catches were done in the same way as those in which hand nets were used, and from May to July 1951 a comparison was made of two different methods: the catchers sitting continuously or sitting and moving alternately. Results for three of the more common species were:—

	Moving	Sitting
Aë aegypti	172	98
Aë. pembaensis	1362	290
Aë. simpsoni	367	140
Totals	1901	528

The significance of these differences has been discussed with reference to *Aë. aegypti* (Teesdale, *l.c.*) and the factors causing them probably also apply to the other two species.

4. Twenty-four hour biting catches.

Three situations were chosen for the 24-hour biting catches, namely: 1, on platforms at different levels in a mango tree; 2, inside houses; 3, outside houses in a village. Fourteen catches were made in each situation. Catches were made monthly throughout the year except for a house catch in November and a village catch (outside) in February. For details of meteorological data for the period of these observations see Teesdale (*l.c.*).

(*1*) *Platforms.*—Two were built, at 30 ft. and 50 ft. above ground, in a large mango tree at Kwa Shekh. Catches were made simultaneously on the ground under the tree and on the platforms. Two assistants, stripped to the waist, caught in each situation in three hour shifts; they captured all mosquitos biting themselves or the back of their partner.

(*2*) *House.*—The first four catches were done in a house at Kwa Shekh and the rest at Jomvu (about 3 miles west of Kwa Shekh) where mosquitos seemed to be more prevalent. Here again two Africans worked together for three-hour periods sitting on the floor and stripped to the waist.

(*3*) *Village.*—The catches were undertaken in an open space surrounded by village houses and were carried out in the same way as those in the house.

TABLE VI.

Results of fourteen 24-hour catches of biting mosquitos at a mango tree at Kwa Shekh, 1950 and 1951.

Time (hr.)	*Aë. aegypti*				*Aë simpsoni*				*Aë. metallicus*				*Aë. pembaensis*				*C. p. fatigans*				*C. duttoni*			
	G	30′	50′	T	G	30′	50′	T	G	30′	50′	T	G	30′	50′	T	G	30′	50′	T	G	30′	50′	T
06–07	3	2	0	5	4	1	2	7	1	2	1	4	192	5	0	197	0	1	1	2	0	0	0	0
07–08	1	0	0	1	3	1	0	4	0	0	0	0	55	7	0	62	0	6	0	6	0	0	0	0
08–09	2	1	0	3	2	2	0	4	0	2	0	2	21	2	3	26	0	0	1	1	0	0	0	0
09–10	1	1	0	2	2	1	0	3	1	2	0	3	11	8	5	24	2	0	0	2	0	0	0	0
10–11	1	1	0	2	1	1	0	2	2	0	0	2	19	4	0	23	0	1	0	1	0	0	0	0
11–12	0	0	0	0	3	2	0	5	1	1	0	2	16	3	0	19	0	6	2	8	0	0	0	0
12–13	0	0	0	0	9	2	0	11	0	0	0	0	45	1	1	47	0	2	0	2	0	0	0	0
13–14	1	2	0	3	2	4	0	6	2	0	0	2	69	2	0	71	5	0	0	5	0	0	0	0
14–15	2	0	3	5	3	1	1	5	0	0	0	0	27	4	1	32	0	2	0	2	0	0	0	0
15–16	2	1	0	3	3	2	0	5	3	0	0	3	34	2	0	36	4	2	0	6	0	0	0	0
16–17	3	5	0	8	6	1	0	7	2	3	0	5	34	0	0	34	0	5	0	5	0	0	0	0
17–18	10	0	0	10	5	9	0	14	6	0	0	6	35	2	0	37	1	1	0	2	0	0	0	0
18–19	7	0	0	7	5	0	0	5	3	0	0	3	150	1	5	156	0	2	0	2	0	3	0	3
19–20	2	0	0	2	0	1	0	1	0	0	0	0	76	6	1	83	1	5	2	8	0	0	1	1
20–21	2	0	0	2	0	0	0	0	0	0	0	0	68	9	2	79	4	9	2	15	1	0	0	1
21–22	0	0	0	0	0	0	0	0	0	0	0	0	145	2	2	149	24	10	8	42	0	0	2	2
22–23	0	0	0	0	0	0	0	0	0	3	0	3	92	8	1	101	13	11	14	38	1	0	0	1
23–00	0	0	1	1	0	0	0	0	0	0	0	0	109	0	0	109	20	7	5	32	0	0	2	2
00–01	0	0	0	0	0	0	0	0	0	0	0	0	58	2	1	61	15	17	9	41	4	4	1	9
01–02	0	0	0	0	0	0	0	0	0	0	0	0	42	2	1	45	40	10	18	68	1	0	3	4
02–03	0	0	0	0	0	0	0	0	1	0	0	1	47	2	1	50	33	20	12	65	5	2	4	11
03–04	0	0	0	0	0	0	0	0	3	0	1	4	110	3	3	116	38	17	13	68	4	2	1	7
04–05	0	1	0	1	0	0	0	0	0	0	0	0	98	8	0	106	19	9	11	39	0	1	2	3
05–06	0	0	0	0	0	0	0	0	1	0	0	1	88	7	26	121	9	5	8	22	0	0	3	3
Totals	37	14	4	55	48	28	3	79	26	13	2	41	1641	90	53	1784	228	148	106	482	16	12	19	47

Also recorded :

Species	Ground	30 ft.	50 ft.	Total
A. gambiae	58	8	3	69
Aë. adersi	2	5	7	14
C. decens	7	1	4	12
T. uniformis	11	1	0	12
C. sitiens	4	2	5	11
T. africanus	2	2	2	6

Species	Ground	30 ft.	50 ft.	Total
A. maculipalpis	2	0	0	2
Aë. fryeri	0	0	2	2
Aë. haworthi	1	0	0	1
Aë. scatophagoides	0	0	1	1
M. brevipalpis	0	1	0	1
Aë. furcifer or *taylori*	0	0	1	1

G = catches on the ground. 30′ = platform 30 ft. above ground. 50′ = platform 50 ft. above ground. T = Total.

TABLE VII.

Results of fourteen 24-hour catches of biting mosquitos in a village. Kwa Shekh (4 catches) and Jomvu Kuu (10 catches), 1950 and 1951.

Time (hr.)	*Aë. aegypti*		*Aë. pembaensis*		*Aë. metallicus*		*Aë. simpsoni*		*C. p. fatigans*		*C. sitiens*		*C. decens*		*C. duttoni*		*C. antennatus*		*A. gambiae*		*A. funestus*		*T. uniformis*		*T. africanus*	
	O	H	O	H	O	H	O	H	O	H	O	H	O	H	O	H	O	H	O	H	O	H	O	H	O	H
06–07 ..	7	4	43	18	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	3	2	1	1	0	0	0
07–08 ..	5	5	15	13	0	0	0	0	0	4	0	0	0	0	0	0	0	0	4	1	3	1	0	0	0	0
08–09 ..	7	4	9	12	0	0	0	0	2	2	1	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0
09–10 ..	11	15	9	4	0	0	0	0	2	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
10–11 ..	10	16	18	4	0	0	0	0	0	1	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
11–12 ..	11	17	8	4	0	0	0	0	6	3	0	0	0	0	0	0	0	0	2	3	0	1	0	0	0	0
12–13 ..	4	7	8	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0
13–14 ..	6	5	9	3	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
14–15 ..	4	6	11	3	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15–16 ..	2	3	8	8	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
16–17 ..	5	2	8	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
17–18 ..	17	5	20	13	0	0	0	0	2	0	0	0	1	0	0	0	5	0	0	0	0	0	0	0	1	0
18–19 ..	9	11	133	8	0	0	0	1	1	2	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
19–20 ..	3	1	44	6	0	0	1	0	1	5	1	0	1	0	2	0	0	0	0	1	0	1	0	0	0	0
20–21 ..	2	0	31	1	0	0	0	0	8	6	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
21–22 ..	2	2	47	10	1	0	0	1	3	6	3	0	0	0	2	0	0	0	6	3	0	0	0	0	1	0
22–23 ..	3	1	54	3	0	0	0	0	11	4	3	0	0	1	4	0	0	0	11	0	1	0	0	0	0	0
23–00 ..	6	0	56	3	0	0	0	0	2	9	3	0	1	0	1	0	0	0	4	3	0	1	0	2	1	0
00–01 ..	3	1	41	18	2	0	0	0	3	8	5	0	0	0	1	0	0	0	5	0	0	1	0	0	0	0
01–02 ..	2	2	31	11	0	0	1	0	3	16	2	0	1	0	0	0	0	0	3	4	0	0	0	0	1	0
02–03 ..	1	0	32	11	0	0	0	0	1	22	1	0	0	2	0	0	0	0	7	5	2	0	0	0	0	0
03–04 ..	1	1	45	3	0	0	0	0	3	7	3	0	0	1	0	0	0	0	8	4	3	0	2	0	0	0
04–05 ..	3	1	23	2	0	0	0	0	2	3	1	0	0	0	0	1	0	0	11	7	0	1	1	0	0	0
05–06 ..	4	1	18	0	0	0	0	0	2	2	2	0	0	0	0	0	0	0	10	12	0	0	2	1	0	0
Total ..	**128**	**110**	**721**	**164**	**3**	**0**	**2**	**2**	**52**	**105**	**33**	**0**	**4**	**4**	**10**	**3**	**5**	**0**	**75**	**49**	**13**	**8**	**6**	**3**	**9**	**0**

O = Outside. H = In a house.

On a few occasions the catchers sat under a large baobab tree as it was thought that more mosquitos might bite during the day in shade, but there was no appreciable difference in the numbers captured. The records are analysed in Tables VI & VII.

Discussion.

Sixty-six species of mosquitos have been recorded in net catches on Mombasa Island and in its surrounding district (Tables I & II) but most of them occur so seldom or in such small numbers that it is not possible to draw any conclusions as to their habits. The following species, which occur commonly, are discussed in some detail:—

Culex pipiens fatigans. This mosquito was taken in greater numbers than any other. Over fifteen thousand examples were captured by hand nets (almost double the number of the next most common species, *Aëdes pembaensis* and *Aë. aegypti*) and it outnumbered other mosquitos in window traps. As it is generally associated with domestic breeding, it was somewhat unexpected to find so many out of doors. Its normal seasonal incidence in Mombasa appears to be greatest from April to August and again from November to December (Table I), during and after the two rainy seasons (April–May, and Oct.–Nov.). It has a great proclivity for pit latrines, septic tanks and sullage pits, and when these contain water in the dry season it may occur in enormous numbers in nearby houses. In biting catches outside during the day it was not common (Table V) but most were taken in October, a month producing comparatively small numbers in net catches. Its seasonal occurrence as shown by window-trap catches followed closely that of net catches in the bush; far larger numbers were always taken during the night (in out-going traps). Comparatively few were found in the entrance traps, where there was generally a preponderance of males during the day, the reverse being the case at night. In the exit traps, females almost always predominated.

The hourly catches (Table IV) show more males in the entry traps up to 21 hr. Activity in the exit traps rose sharply after 18 hr. and remained high for the next three hours. Only weekly examinations were made after 21 hr., but it seems clear that, by 23 hr., activity was decreasing noticeably and remained low until dawn; it then increased again somewhat until about 09 hr. These findings differ from those of van Someren, Heisch & Furlong (1958) at Ganda where 42·5 per cent. left between 02 hr. and dawn.

In 24-hour catches (fig. 1) the same general pattern is seen in bush, house and platforms, with most biting occurring after midnight. This does not coincide with flight activity as shown by the window-trap catches (Table IV) but it agrees broadly with similar captures at Ganda, where the biting peak in bush occurred slightly later than in house or compound. Ground and platform catches show that this mosquito has a preference for biting at ground level (Table VI).

Culex p. fatigans is a truly ubiquitous mosquito at Mombasa, and the observations suggest that there may be an essentially domestic as well as an "outdoor" form.

Culex duttoni was not common; most individuals were taken from April to June and November to December. It was not found biting in bush catches, but occurred in some numbers in one 24-hour catch at the mango tree in November (43 examples out of a total of 47). Biting appears to occur only from dusk to dawn (fig. 1). Two females were taken in window traps.

Culex nebulosus. This species was taken in net catches in every month of the year except May. It was most abundant in July, August and September and again in December. It was not taken in window traps or 24-hour catches; a few individuals were recorded biting in the day-time bush catches in November, December and January.

Culex tigripes was most common in net catches in the bush from May to July and again in December. It was not taken biting or in window-trap captures.

Aëdes simpsoni is an "outdoor" mosquito, only two females being taken inside houses and none in window traps. It was in evidence throughout the year, though scarce in the dry months from January to March. On the coast it breeds mostly in banana leaf axils and pineapple plants (Wiseman & others, 1939;

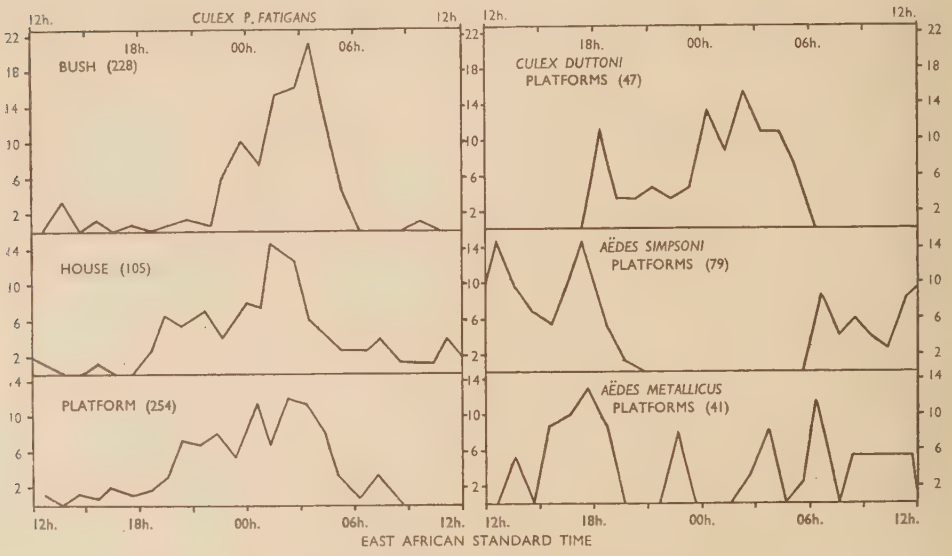


Fig. 1.—The biting cycle of some of the more important mosquitos at Mombasa. Geometric mean numbers biting per hour reduced to a percentage basis. Figures in brackets represent the number of mosquitos captured.

Teesdale, 1941) but also occasionally uses small containers and tree-holes (van Someren, Teesdale & Furlong, 1955). At Kwale (1,200 ft. altitude), about 20 miles south of Mombasa, a seasonal distribution curve for larvae found in banana leaf axils (Teesdale, 1957) shows little relation to distribution as indicated by net catches at Mombasa.

At Kwale, the peak production of larvae in leaf axils occurs in July only, but net catches in Mombasa show two periods of greatest adult abundance—in May and September (fig. 2). This September peak might be explained as a consequence of the earlier larval peak in July, but there is no obvious reason for so large and sudden an increase in May after virtually no breeding in the previous two or three months. Slight differences in climate between Kwale and Mombasa make a true analysis of the two curves difficult.* The seasonal distribution curve derived from diurnal biting in the bush closely parallels that based on net catches, but in the first part of the year most biting occurred a month after highest net captures, whereas in the second part they coincided (September). From September to December, however, there was a gradual falling off in the numbers biting, whereas in the net captures the decrease was much more rapid. In October to December the combination of warmth and humidity is more pronounced and

* Wiseman & others (1939) showed peak breeding at Mombasa in January but this may be due in part to the searchers paying more attention to leaf axils in the dry weather when other foci were scarce.

might account for proportionately more biting (Haddow, 1945*b*). Twenty-four hour catches on platforms and on the ground confirm earlier findings that *Aë. simpsoni* bites almost entirely during daylight and prefers to feed near the ground (Haddow, 1945*a* & *b*; Gillett, 1951; Lumsden, 1955). The catches expressed as geometric means (reduced to a percentage basis) (Haddow, 1954) produced a bimodal type of curve with peak biting between 11 and 13 hr. and from 16 to 18 hr. (fig. 1). Both peaks correspond with findings by Haddow and Lumsden at Bwamba and Taveta, respectively; the reduced period of activity between

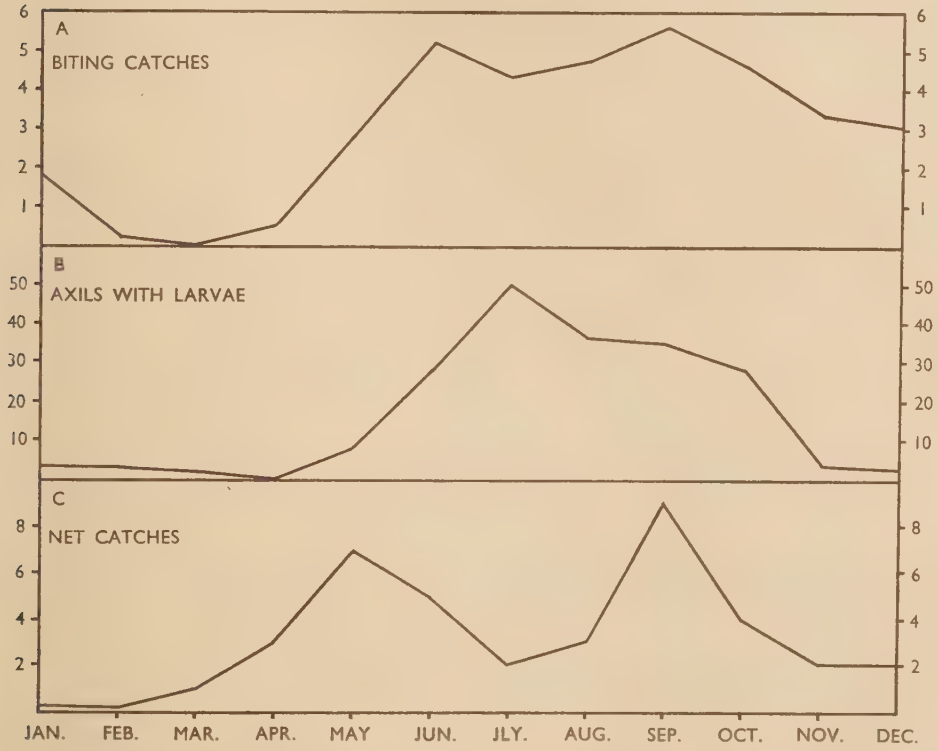


Fig. 2.—Seasonal distribution of *Aëdes simpsoni* based on the catching index derived from (A) daylight biting catches, (B) number of banana leaf axils with larvae, (C) net catches in bush.

10 and 11 hr. also agrees with Lumsden's records at Taveta. Van Someren, Heisch & Furlong (1958) also noticed this lull at Ganda, but there it occurred slightly later; Haddow (1945*b*) also reported the same at Bwamba.

In the daylight biting catches in bush (Table V) the lull in activity came a little earlier (between 09 and 10 hr.) and the morning peak was not evident. In fig. 3, the catching index (derived from the numbers of mosquitos caught biting in the bush) is compared with the geometric mean numbers biting per hour in 24-hour catches (reduced to percentage basis). According to the former, the lull in activity occurs between 08 and 10 hr. and there then follows a sharp increase which is maintained throughout the day with little variation and culminates in an afternoon maximum between 16 and 17 hr. The latter, however, although it also indicates reduced activity in the morning, shows two definite periods of maximum

biting (12–13 hr. and 17–18 hr.) with a distinct falling off between these times. The biting catches in bush continued almost daily for over two years and produced far more mosquitos than the 24-hour catches (3,709 as compared with 79).

Aëdes metallicus. Three hundred and forty-seven examples were captured in diurnal biting catches in the bush (176 during March, April and May—Table V) and 302 by hand nets (193 between May and July—Table I). Some biting also occurred in January. Only four females were found in window traps during the day and one at night. In the 24-hour catches at the mango tree, biting was

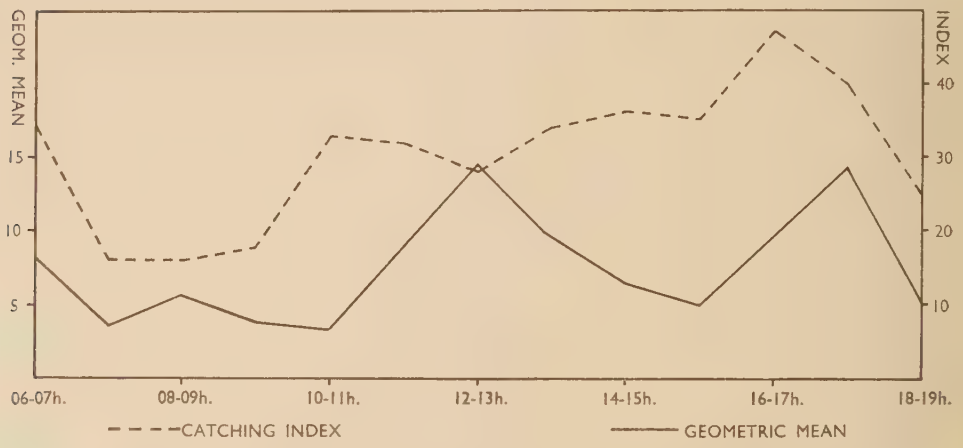


Fig. 3.—Biting activity of *Aëdes simpsoni*. Comparison of geometric mean numbers biting per hour in 24-hour catches with the catching index derived from daylight biting catches in bush.

irregular (fig. 1) but the small numbers indicate peaks of activity at about the same time as recorded by van Someren, Heisch & Furlong (1958) at Ganda (06 hr. and between 15 and 19 hr.). More were captured at ground level than on the platforms although the larvae are commonly found in tree-holes.

Aëdes aegypti. An account of the bionomics of this mosquito has been given elsewhere (Teesdale, 1955). It has been included in fig. 4 and Tables I, III, IV, V, VI and VII for comparison with the other species.

Aëdes pembaensis. This species was very common in the outside biting and net catches. No marked seasonal fluctuations were detected by either method, but most examples were taken in the drier months, *i.e.*, January and July to October. Unlike the other local species (except possibly *Aë. albicosta*) there was no noticeable decline in numbers or activity during the hot dry part of the year from January to March. This may be due to its breeding in sea water in crab-holes, which are more dependent upon tides than rainfall (Goiny, van Someren & Heisch, 1957).

The mosquito also frequents houses, as window-trap catches show (Table III). The writer has on several occasions traced complaints of domestic infestations to this species, especially where houses are built near the foreshore where mangroves (*Avicennia*) are growing. The window traps indicate that both ingress and egress is greatest during the night. Hourly examinations (Table IV) show that most examples of *Aë. pembaensis* leave houses from 18 to 21 hr. and 07 to 08 hr. Between 21 and 07 hr. there were only 11 examinations but they suggest sustained activity throughout the night without marked periods of flight. There was always a pronounced preponderance of females.

In 24-hour catches (fig. 4), the biting rhythm outside shows a nocturnal bimodal curve closely resembling that found in *Avicennia* forest at Gede (Lumsden, 1955); at Kwa Shekh, however, biting took place throughout the 24-hour period and appreciable numbers of adults were captured on the 30-ft. (5%) and 50-ft. (3%) platforms (Table VI).

In the house, the two peak biting periods are less pronounced. Reduced light intensity indoors might be responsible for the more irregular day-time biting.

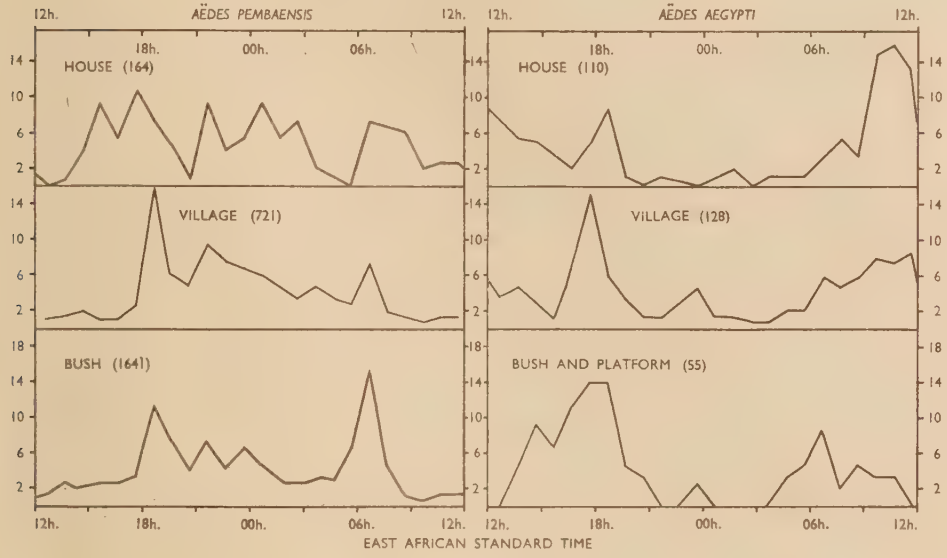


Fig. 4.—The biting cycle of *Aëdes pembaensis* and *Aëdes aegypti* at Mombasa expressed as a percentage of the geometric mean number of mosquitos biting per hour. Figures in brackets represent the number of mosquitos captured.

Aëdes albicosta. It is likely that *Aë. albothorax* (Theo.) has on occasions been mistaken for this species and it is now known that both have been misidentified as *Aë. lineatopennis* (Ludl.) in previous communications (Wiseman & others, 1939; Teesdale, 1950). Mrs. E. C. C. van Someren tells me that the colour variations in this group are confusing but that the great majority of specimens of *Banksinella* captured around Mombasa were of *Aë. albicosta* as described by van Someren, Teesdale & Furlong (1955).

The greatest numbers were taken in December, January and February in outdoor net and biting catches; it is not generally found indoors (van Someren, Teesdale & Furlong, 1955) and was absent in window-trap captures.

The breeding grounds are temporary pools and swamps (Wiseman & others, 1939) but this species has never been found breeding on Mombasa Island and there are few records from the mainland, yet the adults can occur in enormous numbers in the dry weather when they may also infest houses. They are vicious biters (Teesdale, 1950).

Temporary collections of water are most likely to form during the rains of April–May and November–December, and most adults might therefore be expected to occur during or just after these periods; but such is the case only in December and January after the short rains of November and December. At this time the north-east trade winds are blowing strongly, whereas in June–July, after the long

rains, the south-east monsoon becomes established; the presence of *Aë. albicosta* around Mombasa may therefore be related in some way to wind direction; it is known to be a strong flier. Since none was taken in 24-hour catches, the biting rhythm is not known, but 165 specimens were captured in day biting catches in the bush, 49 being taken between 06 and 12 hr. and 116 from 12 to 19 hr.; biting activity was remarkably constant between these latter times; it was least in the late part of the morning.

Aëdes albocephalus. Considerable numbers of this mosquito were taken in bush net catches during and after both rainy seasons. It was not found in window traps. It has been recorded as rarely biting indoors (van Someren, Heisch & Furlong, 1958).

Eretmapodites subsimplicipes. Most examples were collected in net catches in the bush between June and August. Only a few were taken biting in the daytime in the bush; none occurred in 24-hour catches. *E. quinquevittatus* was however more prominent in biting catches; it occurred in greatest numbers in net catches in the bush between April and September.

Anopheles gambiae. In 24-hour catches and net catches in the bush examples of *A. gambiae* were always scarce and occurred rarely in diurnal biting in the bush. In window traps, they were more numerous and there was considerable activity during the day and night; far more were captured in June than in any other month. They appeared suddenly in April and continued until July, when they again disappeared abruptly. Except for a slight temporary increase in December they did not occur again until the following April. In the 24-hour catches, biting began at sunset, increased after midnight and reached its peak just before dawn.

Anopheles funestus. This mosquito was also generally scarce; it occurred rarely in net catches in the bush and was only found biting very occasionally in diurnal catches in the bush. Out of a total of 102 captured at night (see Table III) in window traps between January 1950 and July 1951, 80 were taken in July 1951. At Ganda they also appeared suddenly but there the greatest numbers occurred in December 1951 (van Someren, Heisch & Furlong, 1958). From hourly window-trap captures it was evident that quite a lot of movement took place during the day. There were again only a few in entry traps. In the exit traps there was considerable activity between 07 and 09 hr. and from 18 to 21 hr., but thereafter, until 07 hr., traps were examined once weekly and very few mosquitos were recorded; after 09 hr., activity decreased markedly.

In 24-hour biting catches in the house and village very few examples of *A. funestus* were taken—and none at all at the mango tree.

Summary.

Records are given of the species of mosquitos captured at Mombasa in the years 1943–44 and 1949–52. They were caught by four different methods, namely: (1) day-time net catches in the bush, (2) window-trap catches, (3) diurnal (bait) biting catches in the bush and (4) twenty-four hour (bait) biting catches in three different situations. Sixty-six species were taken in the day-time net catches and nine others which did not figure in the net catches were taken in one or other of the remaining three methods.

The habits of the commonest species, as indicated by these catches, are discussed in some detail.

Culex pipiens fatigans Wied. occurred in large numbers in biting catches, net catches and window-trap catches. In 24-hour catches most biting occurred after midnight, but, in the window traps, activity was greatest between 18 and 21 hr.

Aëdes simpsoni (Theo.) was not taken in window traps or houses. Seasonal occurrence, as indicated by larvae in banana axils, net and biting catches in the bush, is discussed. Twenty-four hour catches confirmed earlier findings that this mosquito bites almost solely during daylight.

Aëdes pembaensis (Theo.) occurred throughout the year with little seasonal variation; this is thought to be connected with its breeding in crab-holes. It is often found in fair numbers in houses when these are near the breeding grounds. Window-trap catches show that most activity takes place at night though some also occurs during the day. The biting rhythm as shown by 24-hour catches in houses, bush and on tree platforms is discussed.

Aëdes albicosta (Edw.). Previously this mosquito may have been confused with *Aëdes albothorax* (Theo.) and *Aë. lineatopennis* (Ludl.). It can occur at times in great numbers when it may bite viciously both indoors and outside.

Anopheles gambiae Giles and *A. funestus* Giles were not evident in large numbers. In window traps most activity took place at night although some also occurred during the day. In 24-hour catches, *A. gambiae* fed mostly just before dawn though biting occurred also from midnight onwards. *A. funestus* appeared suddenly and in fair numbers in window traps but was absent for much of the year.

Aëdes aegypti (L.), though fairly common, is recorded only in Tables and in one figure as its bionomics have already been discussed elsewhere.

Notes are given on other species, which include *Culex duttoni* Theo., *C. nebulosus* Theo., *C. tigripes* Grp., *Aëdes metallicus* (Edw.), *Aë. albocephalus* (Theo.), *Eretmapodites subsimplicipes* Edw. and *E. quinquevittatus* Theo.

Acknowledgements.

I wish to record my sincere thanks to a number of persons who in one way or another have helped me in the compilation of these records; not least among them are the African junior and supervisory staff.

I would particularly thank Mrs. E. C. C. van Someren whose advice has been of the utmost value; Mr. M. Furlong for his help and interest in the field work. Drs. R. B. Heisch and G. S. Nelson for kindly reading and correcting drafts and Mr. L. R. Rickman for drawing the figures.

References.

Gillett, J. D. (1951). The habits of the mosquito *Aëdes* (*Stegomyia*) *simpsoni* Theobald in relation to the epidemiology of yellow fever in Uganda.—*Ann. trop. Med. Parasit.* **45** pp. 110–121.

Goiny, H., van Someren, E. C. C. & Heisch, R. B. (1957). The eggs of *Aedes* (*Skusea*) *pembaensis* Theobald discovered on crabs.—*E. Afr. med. J.* **34** pp. 1–2.

Haddow, A. J. (1945*a*). The mosquitoes of Bwamba County, Uganda. II. Biting activity with special reference to the influence of microclimate.—*Bull. ent. Res.* **36** pp. 33–73.

Haddow, A. J. (1945*b*). The mosquitoes of Bwamba County, Uganda. III. The vertical distribution of mosquitoes in a banana plantation and the biting cycle of *Aëdes* (*Stegomyia*) *simpsoni*, Theo.—*Bull. ent. Res.* **36** pp. 297–304.

Haddow, A. J. (1954). Studies of the biting-habits of African mosquitos; an appraisal of methods employed, with special reference to the twenty-four-hour catch.—*Bull. ent. Res.* **45** pp. 199–242.

Lumsden, W. H. R. (1955). Entomological studies, relating to yellow fever epidemiology, at Gede and Taveta, Kenya.—*Bull. ent. Res.* **46** pp. 149–183.

Teesdale, C. (1941). Pineapple and banana plants as sources of *Aëdes* mosquitoes.—*E. Afr. med. J.* **18** pp. 260–267.

Teesdale, C. (1950). An apparent invasion of *Aëdes* (*Banksinella*) *lineatopennis* and *Aëdes* (*B.*) *albicosta* into Mombasa Island.—*Proc. R. ent. Soc. Lond.* (A) **25** pp. 99–102.

Teesdale, C. (1955). Studies on the bionomics of *Aëdes aegypti* (L.) in its natural habitats in a coastal region of Kenya.—*Bull. ent. Res.* **46** pp. 711–742.

Teesdale, C. (1957). The genus *Musa* Linn. and its rôle in the breeding of *Aëdes* (*Stegomyia*) *simpsoni* (Theo.) on the Kenya coast.—*Bull. ent. Res.* **48** pp. 251–260.

van Someren, E. C. C., Heisch, R. B. & Furlong, M. (1958). Observations on the behaviour of some mosquitos of the Kenya coast.—*Bull. ent. Res.* **49** pp. 643–660.

van Someren, E. C. C., Teesdale, C. & Furlong, M. (1955). The mosquitos of the Kenya coast; records of occurrence, behaviour and habitat.—*Bull. ent. Res.* **46** pp. 463–493.

Wiseman, R. H., Symes, C. B., McMahon, J. C. & Teesdale, C. (1939). Report on a malaria survey of Mombasa.—60 pp. Nairobi, Govt. Printer.

© Commonwealth Agricultural Bureaux, 1959.

AN INVESTIGATION INTO THE POSSIBLE CONTROL OF THE MEALYBUG VECTORS OF CACAO SWOLLEN-SHOOT VIRUS BY TRUNK IMPLANTATION WITH DIMEFOX.

By A. D. Hanna [1] and W. Heatherington [2]

Chesterford Park Research Station, Essex

and

H. R. Mapother [3] and R. Wickens [4]

West African Cocoa Research Institute, Tafo.

It has been shown from the preliminary experiments carried out by Hanna, Judenko & Heatherington (1955) that dimefox (bis(dimethylamino) fluorophosphine oxide), when placed in holes drilled at ground level in cacao trees, gave encouraging results in controlling the three main species of mealybugs that transmit cacao swollen-shoot virus in Ghana, namely *Pseudococcus njalensis* Laing, *Planococcus citri* (Risso) and *Ferrisiana virgata* (Ckll.), of which the first is by far the most common. As the material was placed directly into the trunk, much smaller quantities achieved results similar to those obtained with the soil-application method, which involved considerable waste of material.

As a result of this preliminary work, two further experiments were carried out in 1953, planned to investigate the technique and to determine optimum dosage level. The first of these has been briefly reported by Hanna & Nicol (1954). The present paper comprises details of both the experiments, together with a consideration of their combined results.

First Experiment.

Dosage of dimefox.

Four levels of dosage were used, approximating to $\frac{1}{12}$, $\frac{1}{6}$, $\frac{1}{4}$ and $\frac{1}{3}$ of the soil-application rate, taking this to lie between 700 and 1,200 parts per million for trees of 20–10 in. girth; these dosages were calculated on the estimated weight of the aerial part of the tree, obtained from the known girth—weight relationship (Hanna, Judenko & Heatherington, 1955). The values so calculated were 75, 150, 225 and 300 parts per million (w/w) of 100 per cent. dimefox; these resulted in smaller trees being given an underdose and larger trees a slight overdose relative to fractions of the soil-application rate, as may be seen from Table I.

Placement of dimefox.

The radial and tangential movement of the insecticide inside the tree was considered in addition to the dosage, and the holes were therefore drilled at two spacings, namely, two and four inches between centres, at ground-level round the circumference of the trunk. The wider spacing had been indicated as suitable in the preliminary experiments. The drill size was adjusted so that the required volume of dimefox nearly filled the hole. These were made with a pneumatic

[1] Now at Gezira Research Station, Wad Medani, Sudan.
[2] Now at Royal Agricultural College, Cirencester, Glos.
[3] Now at Long Ashton Research Station, nr. Bristol.
[4] Now at N.A.A.S. Drayton Experimental Husbandry Farm, Stratford-on-Avon.

drill set to a depth of 3·5 in. and directed downwards at an angle of approximately 45° to the main axis of the trunk. A mobile, petrol-engined air compressor mounted on rubber tyres was used. Seven sizes of bit were used, ranging from $\frac{1}{4}$ to $\frac{5}{8}$ in. diameter.

TABLE I.

Dosages in the trunk-implantation method compared with those of soil treatment.

Girth (in.)	Soil–application dosage				
	Normal	1/12th	1/6th	1/4th	1/3rd
10	1135	95	190	285	379
15	826	69	138	207	275
20	757	63	126	189	252
Mean dosage	—	76	151	227	302
Trunk–implantation dosage (present experiment) ..	—	75	150	225	300

Doses in parts per million.

Tree treatment.

The undergrowth was cleared and the base of the tree brushed with a solution of mercuric chloride as an antiseptic measure. Any wood shavings left in the holes were removed by means of a small stick before the insecticide was introduced. Towards the end of the experiment an air-blower attached to the machine was used. The appropriate dose was divided equally between the holes by withdrawing measured aliquot parts of dimefox by means of a hypodermic syringe through a rubber disc covering the mouth of the storage bottle. The holes were sealed by well-fitting wooden plugs 0·5 in. long and covered with molten grafting wax.

Lay-out.

Six blocks of trees selected by visual examination for their high mealybug population were used. Four of these were on the land of the West African Cocoa Research Institute at Tafo and two at Bunso, on the Department of Agriculture plantation. Each block consisted of eight plots of seven trees. The eight treatments (four dosage levels × two hole-spacings) were allocated at random to the eight plots in each block.

With the exception of ten trees between 7 and 10 in. girth, all those treated were of 10 in. girth or more, and all had single stems at ground-level. On the first 28 trees treated, the chupons arising from the base of the trunk were removed in error; on the remainder, they were left. Two of these were over 7 in. girth and received a single injection, while no special action was taken with the smaller ones.

In addition, 42 untreated trees were selected at random around the perimeter of the experimental blocks (28 at Tafo and 14 at Bunso). Of these, 21 were felled at the beginning and 21 at the end of the experiment, and the mealybugs counted. The purpose of this was to follow any change in the mealybug population that might have occurred during the experiment. At Bunso, the seven trees originally selected for examination at the end of the experiment were found to

TABLE II.

The effect of different dosage levels of dimefox, applied by trunk injection at two hole-spacings, on mealybug populations on cacao trees, Tafo and Bunso.
(Counts made 6 weeks after treatment.)

		* Treatment (per 42 trees)								** No treatment (per 7 trees)							
	Dosage level	75 p.p.m.		150 p.p.m.		225 p.p.m.		300 p.p.m.		0 weeks		0 + 6 weeks		0 weeks		0 + 6 weeks	
	Hole-spacing	2 in.	4 in.	2 in.	4 in.	2 in.	4 in.	2 in.	4in.								
Total numbers of mealybugs on different parts of the tree	Canopy	625	723	13	135	67	29	2	7	29598	34752	21673	23429	31240	–	674	6555
	Chupons	3	130	0	0	2	0	6	0	–	–	–	–	–	–	–	–
	Trunk	0	24	0	14	0	3	0	0	1595	2045	2529	2389	1025	–	253	703
	Pods	480	530	196	1340	245	30	42	36	–	–	3124	4028	–	–	42	2830
	Whole tree	1108	1407	209	1489	314	62	50	43	31193	36797	27326	29846	32265	–	969	10088
Extreme numbers on individual trees	Highest	302	216	78	888	98	28	26	24	8791	8401	9725	16656	15204	–	282	2841
	Lowest	0	0	0	0	0	0	0	0	2389	1755	2269	801	27	–	19	233
Average number per tree		26	33	5	35	7	1	1	1	4456	5257	3904	4264	4609	–	138	1441
Site of experiment		T & B	T & B	T & B	T & B	T & B	T & B	T & B	T & B	T	T	T	T	B	–	B	B

* 42 trees in 6 plots of 7 trees for each treatment. ** One plot of 7 trees for each count. T = Tafo, B = Bunso.

have been severely damaged by Mirids, resulting in a very poor canopy, and were therefore discarded. Seven other trees, which had been selected but not used, were available and as they were well scattered throughout the experimental area it was decided to fell and examine them.

Mealybug counts.

Six weeks after treatment, the trees were felled and dissected. Any mealybugs observed were counted, using a binocular microscope, and were classified as adults or nymphs, and according to their location on the tree, that is, on canopy, trunk, chupons or pods. They were not sorted into species.

In all, 336 trees were treated—28 on each of the following days: April 1st, 2nd, 7th–10th, 13th, 14th, 16th, 17th, 20th and 22nd. The examination for mealybugs started on 13th May 1953, six weeks after treatment, and was completed on 4th June, 28 trees also being examined daily. The results of the counts are shown in Table II.

Rainfall.

The amounts of rainfall at the West African Cocoa Research Institute and at Bunso during the course of the experiment were 9·49 and 9·55 in., respectively.

Analysis of results.

The method of analysis appropriate to the 4 × 2 design of the first experiment is described by Cochran & Cox (1957, chap. 5) and has been adhered to throughout. The main effects of doubling the number of drill holes, and of the linear, quadratic and cubic components * of the overall dosage effect and the corresponding components of the interaction effects have all been separately estimated, except where it became obvious that partitioning into three components would still result in their non-significance. All analyses have been carried out after logarithmic transformation, a method first adopted by Williams (1937) for insect population data and now accepted for mealybug data in particular (Strickland, 1951; Cornwell, 1955). For each plot, the mean value of $\log_{10}(n + 1)$ from the seven trees was used, n being the number of mealybugs recorded for any given tree.

TABLE III.

Analysis of variance, first experiment.

Effect	Degrees of freedom	Variance			
		Total bugs	Total adults	Total nymphs	Total bugs (excl. pods)
Replication	5	0·3602	0·0932	0·2956	0·0450
Spacing of holes (H) ..	1	0·0432	0·0239	0·0462	0·0581
Dosage level—linear (L′) ..	1	3·2480***	0·9205***	2·5772***	1·8744***
Dosage level—quadratic (L″)	1	0·4181*	0·1553†	0·3979*	0·6279***
Dosage level—cubic (L‴)	1	0·0522	0·0651	0·0630	0·1485
Interactions— (HL′) ..	1	0·1696			
(HL″) ..	1	0·0102	0·1295	0·2366	0·1548
(HL‴) ..	1	0·1904			
Error	35	0·0811	0·0392	0·0777	0·0426

Levels of significance † 10 per cent. level ($P < 0·10$)
* 5 ,, ,, ,, ($P < 0·05$)
** 1 ,, ,, ,, ($P < 0·01$)
*** 0·1 ,, ,, ,, ($P < 0·001$)

* For an explanation of these terms, see Mather (1949, chap. VIII).

The estimates of the several components of the variance are shown in Table III. The mean values for individual treatments are shown in Tables IV (a–d) for each criterion separately, in terms of single tree results, together with the de-transformed values.

TABLE IV (a–d).

Mean values for the various treatments, first experiment.
Logarithmic values in ordinary type, de-transformed values in heavy type.
Standard errors, etc., in Table IV (e).

Spacing of holes	Total bugs (whole tree) Dosage 75 p.p.m.	150 p.p.m.	225 p.p.m.	300 p.p.m.	Mean	Total adults (whole tree) Dosage 75 p.p.m.	150 p.p.m.	225 p.p.m.	300 p.p.m.	Mean
4 in.	0·753 **4·7**	0·247 **0·8**	0·327 **1·1**	0·135 **0·4**	0·365 **1·3**	0·382 **1·4**	0·127 **0·3**	0·155 **0·4**	0·080 **0·2**	0·185 **0·5**
2 in.	0·952 **8·0**	0·502 **2·2**	0·133 **0·4**	0·115 **0·3**	0·425 **1·7**	0·550 **2·5**	0·275 **0·9**	0·048 **0·1**	0·048 **0·1**	0·230 **0·7**
Mean	0·852 **6·1**	0·374 **1·3**	0·230 **0·7**	0·125 **0·3**	0·395 **1·5**	0·466 **1·9**	0·201 **0·6**	0·102 **0·3**	0·064 **0·2**	0·208 **0·6**
	Total nymphs (whole tree)					Total bugs (excluding those on pods)				
4 in.	0·668 **3·7**	0·223 **0·7**	0·280 **0·9**	0·088 **0·2**	0·315 **1·1**	0·522 **2·3**	0·057 **0·1**	0·137 **0·4**	0·045 **0·1**	0·190 **0·5**
2 in.	0·860 **6·2**	0·397 **1·5**	0·120 **0·3**	0·132 **0·4**	0·377 **1·4**	0·737 **4·5**	0·192 **0·6**	0·057 **0·1**	0·053 **0·1**	0·260 **0·8**
Mean	0·764 **4·8**	0·310 **1·0**	0·200 **0·6**	0·110 **0·3**	0·346 **1·2**	0·629 **3·3**	0·124 **0·3**	0·097 **0·2**	0·049 **0·1**	0·225 **0·7**

The appropriate standard errors and least significant differences at the 5 per cent. level of probability of the means shown in Table IV (a–d) are shown in Table IV (e) in terms of logarithmic values.

TABLE IV (e).

Standard errors of means in Table IV.

Section	Standard Errors (1)	(2)	(3)	Least Sig. Differences (1)	(2)	(3)
a	± 0·116	± 0·058	± 0·082	0·333	0·167	0·235
b	± 0·081	± 0·040	± 0·057	0·233	0·115	0·164
c	± 0·114	± 0·057	± 0·080	0·327	0·164	0·230
d	± 0·084	± 0·042	± 0·060	0·241	0·121	0·172

(1), treatments interaction; (2), spacing; (3), dosage.

From Tables III and IV it may be concluded that the overall response to increasing dosages is of the quadratic form, that is to say, that the regression of the mealybug population (expressed logarithmically as $\log_{10}(n + 1)$) on dosage of dimefox (D) is of the form

$$\log_{10}(n + 1) = a - bD + cD^2$$

Table V confirms the existence of a quadratic response. This Table shows the percentage of " clean " trees in each treatment, a " clean " tree being defined as one bearing no adults and not more than one nymph. There is a lessening of the successive differences from 75 p.p.m. (mean) to 300 p.p.m. (mean), emphasising the unlikelihood of ever attaining 100 per cent. clean trees, even with increased dosages.

TABLE V.

Percentage of clean trees after treatment.

Spacing	Dosage level				Mean
	75 p.p.m.	150 p.p.m.	225 p.p.m.	300 p.p.m.	
4 in.	42·9	73·8	71·4	78·6	66·7
2 in.	38·1	64·3	85·7	85·7	68·4
Mean	40·5	69·0	78·5	82·1	67·5
Differences between successive means	—	28·5	9·5	3·6	—

In no case does the effect of the distance apart of the holes even approach significance, and therefore all subsequent estimates in this experiment have been made using values averaged over the two spacings.

The evidence in favour of a quadratic response allows the setting up of dosage regression equations * and the determination, from these, of the dosage levels that may be expected to ensure that the mean residual population is not above a specified value. A value of not more than one bug per tree has been taken as an arbitrary objective since this closely approximates to mean residual populations recorded by West (1951) in a previous experiment. Table VI shows these equations, together with the expected values at each dosage level and the corresponding de-transformed values. These expected values may be compared with the observed values given in Table IV.

From the equations given in Table VI the theoretical dosages required to produce effective control as recorded by West (1951) may be worked out. These are shown below (Table VII) together with the minimum populations expected.

The reliability of deductions made from the first experiment.

Consideration must be given to the errors attached to estimates based on the regression equations here presented. Retaining the standard of efficacy at a level of an average of not more than one bug per tree, that is, a logarithmic value equal to $\log_{10}2$, the first part of Table VII is drawn up by solution of equations of the form

$$0{\cdot}3010 = k - b_1 d + b_2 d^2$$

* For an explanation of the method of calculating the constants in these equations, see Mather (1949, chap. VIII).

TABLE VI.

Regression equations relating dosage of dimefox and mealybug populations six weeks after treatment, with calculated values of the latter (Experiment I).

Criterion considered	Regression equation giving best fit	Calculated values of population at given dosages							
		75 p.p.m. (E)	75 p.p.m. (D)	150 p.p.m. (E)	150 p.p.m. (D)	225 p.p.m. (E)	225 p.p.m. (D)	300 p.p.m. (E)	300 p.p.m. (D)
Total bugs	$\text{Log}_{10}\ (n+1) = 1{\cdot}4439 - 0{\cdot}6993d + 0{\cdot}0933d^2$	0·838	5·9	0·418	1·6	0·186	0·5	0·140	0·4
Total adults	$\text{Log}_{10}\ (n+1) = 0{\cdot}8218 - 0{\cdot}4180d + 0{\cdot}0575d^2$	0·461	1·9	0·216	0·6	0·085	0·2	0·070	0·2
Total nymphs	$\text{Log}_{10}\ (n+1) = 1{\cdot}3198 - 0{\cdot}6625d + 0{\cdot}0910d^2$	0·748	4·6	0·359	1·3	0·151	0·4	0·126	0·3
Total bugs (excluding those on pods)	$\text{Log}_{10}\ (n+1) = 1{\cdot}2383 - 0{\cdot}7486d + 0{\cdot}1144d^2$	0·604	3·0	0·199	0·6	0·22	0·1	0·074	0·2

n = number of individuals per tree ; d = dose (as multiple of 75 p.p.m.); (E) = Expected logarithmic values of population per tree at the given dosage ; (D) = De-transformed value of E.

giving upper and lower values for d, the lower of which is recorded in the Table. However, this procedure only defines the mean population value, with no indication of the range of the population about the theoretical value of unity. It is required to define a dose that will ensure that not more than a limited percentage of future observations will be above the value unity. This is achieved by

TABLE VII.

Theoretical dosages of dimefox required for effective control.

Criterion considered	Dose for effective control (p.p.m.)	Minimum population values		Dose to achieve minimum values (p.p.m.)
		Log.	Arith.	
Total bugs	181	0·1336	0·36	281
Total adults	—	0·0621	0·15	273
Total nymphs ..	166	0·1140	0·30	273
Total bugs (excl. those on pods)	129	0·0136	0·03	245

" Effective control " required the complete absence of adults; this is not possible here since the minimal population value is 0·15 adult per tree.

modifying the regression equations to take account of the confidence limits of estimates made from them. With a limit l, the equations take the form

$$0{\cdot}3010 - l = k - b_1 d + b_2 d^2$$

The value of l is found as $l = st$ where t is taken from tables and s is the residual error in the regression analyses after removing the linear and quadratic components. These analyses are summarised in Table VIII.

TABLE VIII.

Factors	Degrees of freedom	Sums of Squares		
		Total bugs	Total nymphs	Total bugs (excluding those on pods)
Regressions ..	2	3·6661	2·9779	2·5009
Residual ..	45	5·1058	4·5411	2·0783
Total ..	47	8·7719	7·5190	4·5792

No further consideration has been given to " Total adults " because of the impossibility of achieving an effective control (Table VII).

Using the 10 per cent. value of t at 45 degrees of freedom, thus estimating for not more than 5 per cent. of future observations lying above $\log_{10}2$, it is found that the upper limits are as follows:

Total bugs	+ 0·5660
Total nymphs	+ 0·5337
Total bugs excluding pods	+ 0·3601

Since all these are greater than $\log_{10}2$ it follows that for this level of control the curves must be capable of reaching negative logarithmic values. The minimum points on the curves have been demonstrated (Table VII) and all are positive, hence such a degree of control appears impossible. The proportion of expected values lying between the minimum value and $\log_{10}2$ can, however, be estimated as

$$\frac{\log_{10}2 - \text{min. value}}{s} = t$$

whence a value for P can be obtained from tables (Fisher & Yates, 1953). It is seen in this way that the percentage of observations expected to be above $\log_{10}2$ is 35, 30 and 10, respectively, for total bugs, total nymphs, and total bugs excluding those on pods.

Thus, the conclusion must be put forward that although average residual populations within the limits prescribed for effective control may be expected, the probability of variation about these averages is extremely high, although this variation is reduced when bugs on pods are not considered.

Second Experiment.

The second experiment was carried out at the West African Cocoa Research Institute, Tafo, with the objects of verifying the results of the previous experiment and testing the efficiency of the treatment during a rainy season (September–November 1953).

From consideration of the results of the first experiment, it would appear that a greater measure of control might be obtained with a dosage level of 375 p.p.m. Further, it was considered worth while examining the effect of increasing the period between tree treatment and mealybug count. An arbitrary extension of three weeks was made. Since little difference in effect had been apparent between the two spacings of the implantation holes, it was decided to space all these at 4 in. The method of placement of dimefox and tree treatment was the same as in the first experiment.

Experimental procedure.

The dosage levels of dimefox used were the same as in the first experiment, with the addition of 375 p.p.m.

Four blocks of cacao trees were selected as before. Each block consisted of 10 plots of seven trees. The 10 treatments (5 dosage levels each examined at 6 and 9 weeks) were allocated at random to the 10 plots in each block. Change in the mealybug population was followed on 21 trees scattered throughout the experimental area. Of these, seven were examined directly before treatment started, seven after six weeks and seven after nine weeks.

Counts of mealybugs were made as before after the appropriate intervals (6 and 9 weeks after treatment) and the results are shown in Table IX.

The amount of rainfall during the course of this experiment was 3·40 in. It was unfortunate that this quantity was much less than that recorded during the first experiment.

Analysis of results.

Analyses of variance over all forty plots of the second experiment were only carried out for " total bugs excluding those on pods ", and it at once became obvious that the nine-week plots showed significantly higher populations than the six-week plots. Subsequently a subsidiary form of the analysis of variance was set up for the six-week plots only. The results of these two sets of analyses are summarised in Tables X and XI.

TABLE IX.

The effect of different dosage levels of dimefox, applied by trunk injection, on mealybug populations on cacao trees, Tafo.

(Counts made 6 and 9 weeks after treatment.)

	* Treatment (per 28 trees)										** No treatment (per 7 trees)		
	Dosage level	75 p.p.m.		150 p.p.m.		225 p.p.m.		300 p.p.m.		375 p.p.m.		0 weeks	0 + 6 weeks	0 + 9 weeks
	Treatment period	6 weeks	9 weeks	6 weeks	9 weeks	6 weeks	9 weeks	6 weeks	9 weeks	6 weeks	9 weeks			
Number of mealybugs on the :—	Canopy	3466	7028	560	3316	64	1202	94	654	9	350	6201	4570	15781
	Chupons	48	172	178	85	1	145	9	30	192	16	32	0	424
	Trunk	57	48	1	18	0	3	1	7	2	8	736	115	474
	Pods	142	268	132	63	6	23	125	75	14	65	307	329	213
	Whole tree	3713	7516	871	3482	71	1373	229	766	217	439	7276	5014	16892
Extreme numbers on individual trees	Highest	986	990	124	390	33	391	81	165	117	199	3311	1749	3163
	Lowest	0	6	0	0	0	0	0	0	0	0	13	227	1915
Av. number per tree		133	268	31	124	3	49	8	27	8	16	1039	716	2413

* 28 trees in 4 plots of 7 trees for each treatment.

** One plot of 7 trees for each count.

Mean values and standard errors may be derived from these two Tables, but they are not presented here. The main interest lies in the quadratic response, although the level of significance reached by this component ($P < 0{\cdot}1$) is not so high as in Experiment I ($P < 0{\cdot}05$).

TABLE X.

Analysis of variance, including effect of time of examination (six and nine weeks).

Effect	D.F.	Variance	
		Total bugs	Total bugs (excluding those on pods)
Replications	3	0·2295	0·2330
Time (T)	1	3·2490***	3·3120***
Dosage level –linear (L′) ..	1	8·8578***	9·1666***
–quadratic (L″)	1	1·726	1·3202
–cubic (L‴) ..	1		
–quadratic (L⁗)	1		
TL′	1	0·5411	0·6109
TL″	1		
TL‴	1		
TL⁗	1		
Error	27	0·233819	0·233215

TABLE XI.

Analysis of variance (six-week plots only).

Effect	D.F.	Variances			
		Total bugs	Total adults	Total nymphs	Total bugs (excluding those on pods)
Replications	3	0·2535	0·1259	0·2087	0·2907
L′	1	3·4398***	1·2960**	3·1979**	3·3005***
L″	1	0·7944†	0·3878†	0·7200†	0·8331*
L‴	1	0·5144	0·0773	0·4476	0·2999
L⁗	1			0·4432	
Error	12	0·176350	0·098875	0·163342	0·159650

Levels of significance † 10 per cent. level ($P < 0{\cdot}10$)
* 5 ,, ,, ,, ($P < 0{\cdot}05$)
** 1 ,, ,, ,, ($P < 0{\cdot}01$)
*** 0·1 ,, ,, ,, ($P < 0{\cdot}001$)

The regression equations set up for the six-week examination periods only in Experiment II, with the quadratic element included in each case, are shown in Table XII.

The theoretical dosages required to produce " effective " control together with minimum expected population values and the corresponding doses may be deduced from the equations and are shown in Table XIII.

It may be shown by a method similar to that used in Experiment I that it is not possible to achieve more than an average effective control and that there can be no question of, say, 95 per cent. of observations lying below $\log_{10}2$. The

TABLE XII.

Regression equations relating dosage of dimefox and mealybug populations six weeks after treatment, with observed and calculated values of the latter (Experiment II).

Criterion considered	Regression Equation giving best fit	(1)			(2)			(3)			(4)			(5)		
		75 p.p.m. (O)	(E)	(D)	150 p.p.m. (O)	(E)	(D)	225 p.p.m. (O)	(E)	(D)	300 p.p.m. (O)	(E)	(D)	375 p.p.m. (O)	(E)	(D)
Total bugs	$\text{Log}_{10}(n+1) = 2{\cdot}4171 - 1{\cdot}0079d + 0{\cdot}1191d^2$	1·512	1·528	32·7	0·992	0·878	6·6	0·215	0·465	1·9	0·510	0·291	0·9	0·288	0·355	1·3
Total adults	$\text{Log}_{10}(n+1) = 1{\cdot}4272 - 0{\cdot}6793d + 0{\cdot}0832d^2$	0·800	0·831	5·8	0·490	0·401	1·5	0·043	0·138	0·4	0·079	0·041	0·1	0·106	0·111	0·3
Total nymphs	$\text{Log}_{10}(n+1) = 2{\cdot}2949 - 0{\cdot}9631d + 0{\cdot}1134d^2$	1·440	1·445	26·9	0·912	0·822	5·6	0·188	0·426	1·7	0·485	0·257	0·8	0·240	0·314	1·1
Total bugs (excluding those on pods) ..	$\text{Log}_{10}(n+1) = 2{\cdot}3390 - 1{\cdot}0190d + 0{\cdot}1220d^2$	1·432	1·442	26·7	0·872	0·789	5·2	0·190	0·380	1·4	0·385	0·215	0·6	0·240	0·294	1·0

n = number of individuals per tree. d = dose (as multiple of 75 p.p.m.)
(O)—Observed logarithmic value per tree
(E)—Expected " " " " } at the given dosage.
(D)—De-transformed value of E

proportions of observations expected to lie above this effective control level are 50 per cent. for total bugs and total nymphs and 45 per cent. for total bugs (excluding those on pods). In other words, the minimum values are so near $\log_{10}2$ as to make little if any difference in the distribution of residual populations when doses expected to give the minimum populations are applied.

TABLE XIII.

Criterion considered	Dose for effective control		Minimum expected population values		Dose to achieve these minimum values (p.p.m.)
	"Level"	p.p.m.	Log.	Arith.	
Total bugs	3·86	290	0·2847	0·93	317
Total adults	—	—	0·0406	0·10	306
Total nymphs ..	3·44	258	0·2500	0·79	318
Total bugs (excluding those on pods) ..	3·32	249	0·2112	0·63	313

Analysis of the Combined Results of the two Experiments.

The experiments were of a different layout but had two factors in common, since both allowed an investigation of the dose range 75–300 p.p.m. by increments of 75 p.p.m., using a minimum number of drill holes, and both had at least four replicates of these treatments. Although Experiment I had six replicates, two were on a second site using rather older cacao trees, which showed lower initial populations. The first four replicates of Experiment I and the whole of Experiment II were sited in the same area of cacao on the Institute's land at Tafo. One may therefore look at differences between experiments (taking only those

TABLE XIV.

Combined analysis of variance, Experiment I (4 replicates only) and Experiment II, Tafo.

Effect	D.F.	S.S.	M.S.	F
Between experiments ..	1	0·9350	0·9350	7·38*
Replications within Expt. I	3	1·4838		
Replications within Expt. II	3			
Treatments (Dosage levels)				
Linear	1	3·4135	3·4135	26·95***
Quadratic	1	0·6933	0·6933	5·47*
Cubic	1	0·0052		
Treatments × Expts. ..	3	0·9925	0·3308	2·61 n.s.
Residual	18	2·2796	0·126644	
Total	31	9·8029		

Symbols as for Table XI (n.s.—not significant).

factors in common) as some measure of seasonal differences, and the following analysis of variance can accordingly be set up. This relates only to total bugs on all parts of the tree, since this must be the final criterion of efficacy.

Since from Table XIV it is seen that the difference between experiments reaches significance there is little to be gained by setting up a pooled regression equation. The non-significance of the Treatments × Experiments interaction is noteworthy, implying as it does that the treatments have produced the same type of response in both cases, but one that is of a different order from the between-treatments effect, which is significant. Calculations based on the dosage-regression equations show that a given dose in October–November is about half as effective, in terms of residual populations expressed logarithmically, as the same dose given in April–May.

The possibility exists that natural population differences may well account for this effect. Examination of Table XV shows that although the October–November populations were lower than those of April–May and were fairly well stabilised, the latter were falling.

TABLE XV.

Natural populations of mealybugs on untreated cacao trees, Tafo, 1953.

Date	Mean logarithmic populations on seven random untreated trees
March 31st ..	3·73
April 6th ..	3·55
May 12th ..	3·53
May 20th ..	3·41
October 10th ..	2·71
October 28th ..	2·78
November 25th ..	2·79

The coefficient of the linear regression of the April–May values of the population against the logarithm of time from March 30th (in days) is −0·1527 and is significant at the 10 per cent. level of probability.

If the October–November natural population is regarded as a stable one, it would seem appropriate to correct the April–May figures for residual populations on treated trees by adding 0·1527 for each unit change in the logarithm of the time (in days) from March 30th to the examination date. This represents an average correction of 0·26 (as $\log(n + 1)$) per tree. A repetition of the analysis set out in Table XV, using these corrected values, reduces the total sum of squares to 8·9215 and the "Between experiments" variance to 0·0536, which does not reach significance. This implies that the naturally falling population of Experiment I had a marked effect in producing the lower residual populations there. Accordingly it appears that the best estimate of the response curve is that obtained by taking corrected values from Experiment I and observed values from Experiment II. The regression equation is found to be

$$\mathrm{Log}_{10}(n + 1) = 2{\cdot}2328 - 1{\cdot}0281d + 0{\cdot}1472d^2$$

This has a minimum value at $d = 3{\cdot}49$ (presenting 261 p.p.m.), when $\log_{10}(n + 1) = 0{\cdot}4376$, or $n = 1{\cdot}7$ bugs per tree; the 95 per cent. upper confidence limit remains very high at +0·6915. This result confirms the expected unreliability of guaranteeing effective control.

While discussing natural populations, it is perhaps of interest to compare the mean residual population at the six- and nine-week examination dates with the natural populations observed on or about those dates (Table XVI).

TABLE XVI.

Changes in natural populations compared with those on treated trees.

Residual populations on treated plots						
Serial No.	Six-week examination	Date	Nine-week examination	Date	Natural population	Date
I ..	0·54	26–27/11	1·68	17–18/12	2·79	25/11
II ..	0·79	30/11–1/12	1·23	21–22/12	—	—
III ..	1·22	2–3/12	1·58	23–24/12	—	—
IV ..	0·69	7–8/12	1·21	28–29/12	3·39	30/12

The average increase in population per tree in the three-week interval between examinations is 0·61 (as $\log(n + 1)$), whereas the total increase in the natural population during the five-week period covering these examination dates is 0·60. There is, therefore, no indication that the build-up rate of population on treated trees has been diminished, but rather a suggestion that it may have been accelerated.

Phytotoxic Effects.

Slight leaf-shedding occurred in some trees, especially those treated with high dosages. When freshly cut, six weeks after treatment, the stumps of the treated trees showed irregularly shaped areas that were discoloured brown. These areas were wet and a liquid continued to seep from them.

In longitudinal sections of the trunk and tap root, the discoloration was roughly diamond-shaped, being widest at the position of the holes and narrowing to a point about 18 in. above each hole and 6 in. below it. The discoloration was mainly brown, but around the holes it was purple. In several cases, a clear liquid remained in the holes. It must be pointed out that the dimefox used contained a purple dye.

Portions of the trunk and the tap root of treated and untreated trees from the first experiment were sent by air to the United Kingdom for examination at the Forest Products Research Station, Princes Risborough, to the staff of which the authors are indebted for the appraisal that follows.

Dead cells were observed in the discoloured areas of the wood of the treated trees and also, but to a lesser extent, in the areas where the wood was normal in colour. The protoplasm of the xylem ray and parenchyma cells in the discoloured areas was abnormal and appeared to contain degeneration products, many of these being round bodies staining with safranin. It was thought that the cells in the stained area were mostly dead or moribund. Degeneration products were not observed in the normally coloured areas of the treated tree. The middle lamella also appeared to have been affected, either directly or indirectly by injection, as many cells in the discoloured areas were separated from each other. There was no evidence of fungal invasion.

In the untreated trees, some few dead cells were present in the discoloured area of the wood, otherwise everything appeared normal.

Summary.

Preliminary experiments having shown that dimefox (bis(dimethylamino) fluorophosphine oxide) placed in holes drilled at ground-level in cacao trees gave encouraging results in controlling the most important of the mealybugs that transmit swollen-shoot virus (*Pseudococcus njalensis* (Laing), *Planococcus citri* (Risso) and *Ferrisiana virgata* (Ckll.)), two further experiments to investigate the technique and determine the optimum dosage were performed in Ghana in April–June and September–November 1953, respectively. A randomised-block layout was used, with four replicates (each comprising a plot of seven trees) of each treatment at Tafo and, in the first experiment, another two at Bunso. The first experiment disclosed no significant difference in effect when the implantation holes were spaced four inches as against two inches between centres and the former spacing alone was used in the second experiment. The dosage levels of dimefox, based on the weight of the aerial part of the tree estimated from the girth—weight ratio, were 75, 150, 225 and 300 parts per million w/w in each experiment, the lowest representing about one-twelfth of the soil-application rate, and also 375 p.p.m. in the second experiment. The results were assessed in terms of the total number of mealybugs, of all three species, counted on the various parts of the trees, which were felled and examined six weeks after treatment; counts made on a duplicate set of trees in the second experiment that were felled at nine weeks were significantly greater.

Statistical analyses of the logarithmic transformations of the population figures obtained at six weeks showed the regression of population on dosage to be a curve of quadratic form. There was thus a limit to the response obtained, the minimum populations of total mealybugs (adults + nymphs) being achieved at a dose rate of 281 p.p.m. in the first experiment and 317 p.p.m. in the second. In the former, the minimum value of the average population of total mealybugs per tree was below that required for efficient control (one per tree), but the variability of the response was such that the population on 35 per cent. of trees so treated would have been above that level; in the latter, the minimum average value attainable was only slightly less than one, and consequently the population on nearly half the trees would have exceeded the level for effective control. Analysis of the combined results from those replications of each experiment that were sited at Tafo showed that a given dosage rate appeared only about half as effective, in terms of the residual population (expressed logarithmically), in October–November as in April–May, but concurrent records from untreated control trees suggest that this may partly have been because populations were falling naturally at the earlier date. Slight leaf-shedding occurred in some of the treated trees.

Acknowledgements.

The authors are indebted to the Directors of Fisons Pest Control Limited, Cambridge, and to the Director of the West African Cocoa Research Institute, Tafo, Ghana, for permission to publish these results. We are also obliged to Mr. W. Caughey, Mrs. W. Heatherington, Mr. F. E. Decker, Mr. Osae and Mr. Owusu Kredua, who ably assisted us in field and laboratory work.

References.

Cochran, W. G. & Cox, G. M. (1957). Experimental designs.—2nd edn., 611 pp. New York, Wiley; London, Chapman & Hall.

Cornwell, P. B. [1955]. Mealybug population, distribution and migration.—*Proc. W. Afr. int. Cacao Res. Conf. 1953* pp. 8–17.

FISHER, Sir R. A. & YATES, F. (1953). Statistical tables for biological, agricultural and medical research.—4th edn., 126 pp. Edinburgh, Oliver & Boyd.

HANNA, A. D., JUDENKO, E. & HEATHERINGTON, W. (1955). Systemic insecticides for the control of insects transmitting swollen-shoot virus disease of cacao in the Gold Coast.—*Bull. ent. Res.* **46** pp. 669–710.

HANNA, A. D. & NICOL, J. (1954). Application of systemic insecticide by trunk implantation to control a mealybug vector of cacao swollen shoot virus.—*Nature, Lond.* **173** pp. 730–731.

MATHER, K. (1949). Statistical analysis in biology.—3rd edn., 267 pp. London, Methuen.

STRICKLAND, A. H. (1951). The entomology of swollen shoot of cacao. II The bionomics and ecology of the species involved.—*Bull. ent. Res.* **42** pp. 65–103.

WEST, J. [1951]. Progress of work at WACRI on systemic insecticides carried out with Pest Control, Ltd.—*Rep. Cocoa Conf. 1951* pp. 86–92.

WILLIAMS, C. B. (1937). The use of logarithms in the interpretation of certain entomological problems.—*Ann. appl. Biol.* **24** pp. 404–414.

© Commonwealth Agricultural Bureaux, 1959.

OBSERVATIONS ON THE MOSQUITO, *AEDES* (*STEGOMYIA*) *AEGYPTI* (L.), IN EAST AFRICA.

I.—THE BITING CYCLE IN AN OUTDOOR POPULATION AT ENTEBBE, UGANDA.

By G. A. H. McClelland

East African Virus Research Institute, Entebbe, Uganda.

Well-defined cyclical biting activity has been found to occur in six species of *Aëdes* in the subgenus *Stegomyia*. Haddow (1945) showed it in the case of *A. simpsoni* (Theo.); Haddow, Gillett & Highton (1947) found it in *A. apicoargenteus* (Theo.) and most clearly of all in *A. africanus* (Theo.). Mattingly (1949) obtained similar results with *A. africanus* in West Africa. Haddow & van Someren (1950) found an indication of similar activity in *A. ruwenzori* Haddow & van Som., *A. bambusae* Edw. and *A. angustus* Edw. Recent work has shown the oviposition cycle to be equally well defined in the case of both *A. africanus* (Gillett & Haddow, 1957) and *A. aegypti* (Haddow & Gillett, 1957). It is therefore surprising that the relatively little work on the biting activity of such an important species as *A. aegypti* has led to somewhat conflicting results. The desirability of further study is stressed by Haddow & Gillett (1957).

Teesdale (1955) working on the Kenya coast, took small numbers of *A. aegypti* over a long period in four series of catches both indoors and out of doors, and found evidence of morning and afternoon peaks. Van Someren, Heisch & Furlong (1958) working at Ganda, also on the Kenya coast, obtained an essentially similar picture. Lumsden (1957) in Tanganyika, obtaining very large numbers in only two days' catch in and around a hut, found as many as six peaks of activity, indicating a rather vague but generally diurnal pattern.

The present paper presents the results of ten 24-hour catches in Uganda, together with observations on flight activity, on a population of *A. aegypti* the majority of which are referable to subsp. *formosus* (Wlk.), which, it is felt, provide the clearest picture of well-defined cyclical activity so far available.

Locality.

The work took place at Bunono, a small lateritic arm of the Entebbe peninsula extending into a swamp in Waiya Bay of Lake Victoria. A strip of forest, varying in width from 0–300 metres, separates the swamp from an area of mixed peasant cultivation of bananas, sweet potatoes, cassava and other crops, interspersed with clumps of elephant grass (*Pennisetum purpureum*) and sword grass (*Imperata cylindrica* var. *africana*). Houses are fairly evenly distributed, with a mean density of 3·8 per hectare in this cultivated area. At the single point where a break in the forest gives easy access to the swamp, there is a recently derelict sawmill, where, in large numbers of old tyres and abandoned vehicles, is the richest focus of *A. aegypti* so far discovered in the Entebbe area by the writer. A site shaded by some banana plants, about 20 m. from this focus and the forest edge, was chosen for a series of 24-hour catches.

Methods.

Biting activity (*including alighting of males on bait*).

The method of catching mosquitos in individual tubes, over a continuous period of 24 hours or more, follows that of Haddow (1945, 1954). The catching

team consisted of three active members who caught any mosquito alighting on themselves or on each other. Each hour, one member was replaced from a reserve of two or three. Thus the catches employed five or six men with an African supervisor. The writer was present, or paid visits, for much of the time.

The catches were divided into hourly groups, and, following the method of Lumsden (1952), East African Standard Time was adjusted to give a "catch time" in which sunset always occurred at 18 hr. (and thus sunrise at about 06 hr.). Five single 24-hour catches, one 48-hour catch and one 72-hour catch were made, but these are treated here as ten 24-hour catches. Catching was in every case begun one hour before the recorded start, and the first hour's catch discarded. This should have eliminated possible anomalies due to abnormal biting behaviour caused by the arrival of the catching team. If this precaution is taken, the time of starting should, in practice, be irrelevant. Starting times were 12, 10, 11 and 09 hr., respectively, for the first four catches and 18 hr. for the remainder.

Flight activity.

Following a chance observation of intense flight activity as the final 72-hour catch started, it was decided to make periodic estimates, during daylight, of the numbers of *A. aegypti* flying over a group of water-filled tyres near the 24-hour catch site. Observations started at 1030 hr. the following day and continued at 10, 30 and 50 minutes past each hour (catch time) between 0550 and 1810 hr. until three days had been covered. Note was made of swarming, a rhythmic dancing flight of several males and females, distinct from the meandering flight of single individuals that was more usual.

Of the 114 observations, 73 were made by the writer personally, and the remainder by the African supervisor. The writer made, during the whole period, at least one observation at each time, and there was no apparent disagreement between the two observers. With the exception of the final period from 0550 to 1000, these counts were contemporaneous with the 72-hour catch, and 25 m. away from it.

Analysis.

The geometric mean (M_6) as used by Williams (1937), multiplied by 100 and expressed as a percentage (Haddow, 1954), has been calculated in every case. It is applied to the flight-activity figures in the form of a running mean over three consecutive counts, corresponding values for the three days being combined. These smoothed geometric means of nine values were then grouped arithmetically into hours for comparison with the biting figures (which are not smoothed means).

Results.

Biting activity.

The total mosquitos taken alighting on the bait in the series were as follows:—

	Females	Males
Anopheles (*Anopheles*) *coustani* var. *ziemanni* (Grünb.) ...	6	–
Hodgesia cyptopus Theo.	41	–
Ficalbia (*Mimomyia*) *femorata* Edw.	1	–
Mansonia (*Coquillettidia*) *fuscopennata* (Theo.)	2,105	–
Mansonia (*Mansonioides*) *africana* (Theo.)	5,161	–
Mansonia (*Mansonioides*) *uniformis* (Theo.)	1,691	1
Aëdes (*Stegomyia*) *aegypti* (L.)	238	26
Aëdes (*Stegomyia*) *apicoargenteus* (Theo.)	1	–
Culex (*Culex*) *annulioris* var. *consimilis* Newst.	10	–
Totals	9,254	27

TABLE I.

Distribution, between the ten 24-hour periods, of the 264 examples of *A. aegypti* taken alighting on the bait.

Five single 24-hr. periods			One 48-hr. and one 72-hr. period		
Dates	Males	Females	Dates	Males	Females
11.iv.57 ..	1	27	12.ii.58 ..	1	32
16.iv.57 ..	—	30	13.ii.58 ..	1	20
9.i.58 ..	15	33	18.ii.58 ..	1	4
23.i.58 ..	—	42	19.ii.58 ..	6	19
5.ii.58 ..	1	22	20.ii.58 ..	—	9
Totals ..	17	154	Totals ..	9	84

The distribution of the 264 examples of *A. aegypti* between the ten 24-hour periods is shown in Table I. The hourly results and means are shown separately for males and females in Table II and the percentage geometric means for

TABLE II.

Total catches and geometric means per hour of males and females of *A. aegypti* taken alighting on the bait in the ten 24-hour periods.

	Females				Males			
Hour	No.	No. of days	$M_G \times 100$	M_G%	No.	No. of days	$M_G \times 100$	M_G%
00–01 ..	2	2	15	1·0	0	0	0	0·0
01–02 ..	0	0	0	0·0	0	0	0	0·0
02–03 ..	0	0	0	0·0	0	0	0	0·0
03–04 ..	0	0	0	0·0	0	0	0	0·0
04–05 ..	0	0	0	0·0	0	0	0	0·0
05–06 ..	0	0	0	0·0	0	0	0	0·0
sunrise								
06–07 ..	2	1	12	0·8	0	0	0	0·0
07–08 ..	4	3	28	1·8	0	0	0	0·0
08–09 ..	19	5	101	6·6	3	1	15	1·0
09–10 ..	4	4	32	2·1	0	0	0	0·0
10–11 ..	5	3	32	2·1	0	0	0	0·0
11–12 ..	9	4	50	3·2	0	0	0	0·0
12–13 ..	11	4	62	4·1	0	0	0	0·0
13–14 ..	11	5	66	4·3	0	0	0	0·0
14–15 ..	16	3	63	4·1	0	0	0	0·0
15–16 ..	39	5	188	12·3	10	2	35	2·3
16–17 ..	63	10	485	31·8	10	6	69	4·5
17–18 ..	45	8	338	22·2	3	2	20	1·3
sunset								
18–19 ..	7	4	47	3·1	0	0	0	0·0
19–20 ..	0	0	0	0·0	0	0	0	0·0
20–21 ..	0	0	0	0·0	0	0	0	0·0
21–22 ..	1	1	7	0·5	0	0	0	0·0
22–23 ..	0	0	0	0·0	0	0	0	0·0
23–24 ..	0	0	0	0·0	0	0	0	0·0

Note: The geometric mean percentage for males has been calculated from M_G using the female percentage factor to preserve the relative difference between male and female.

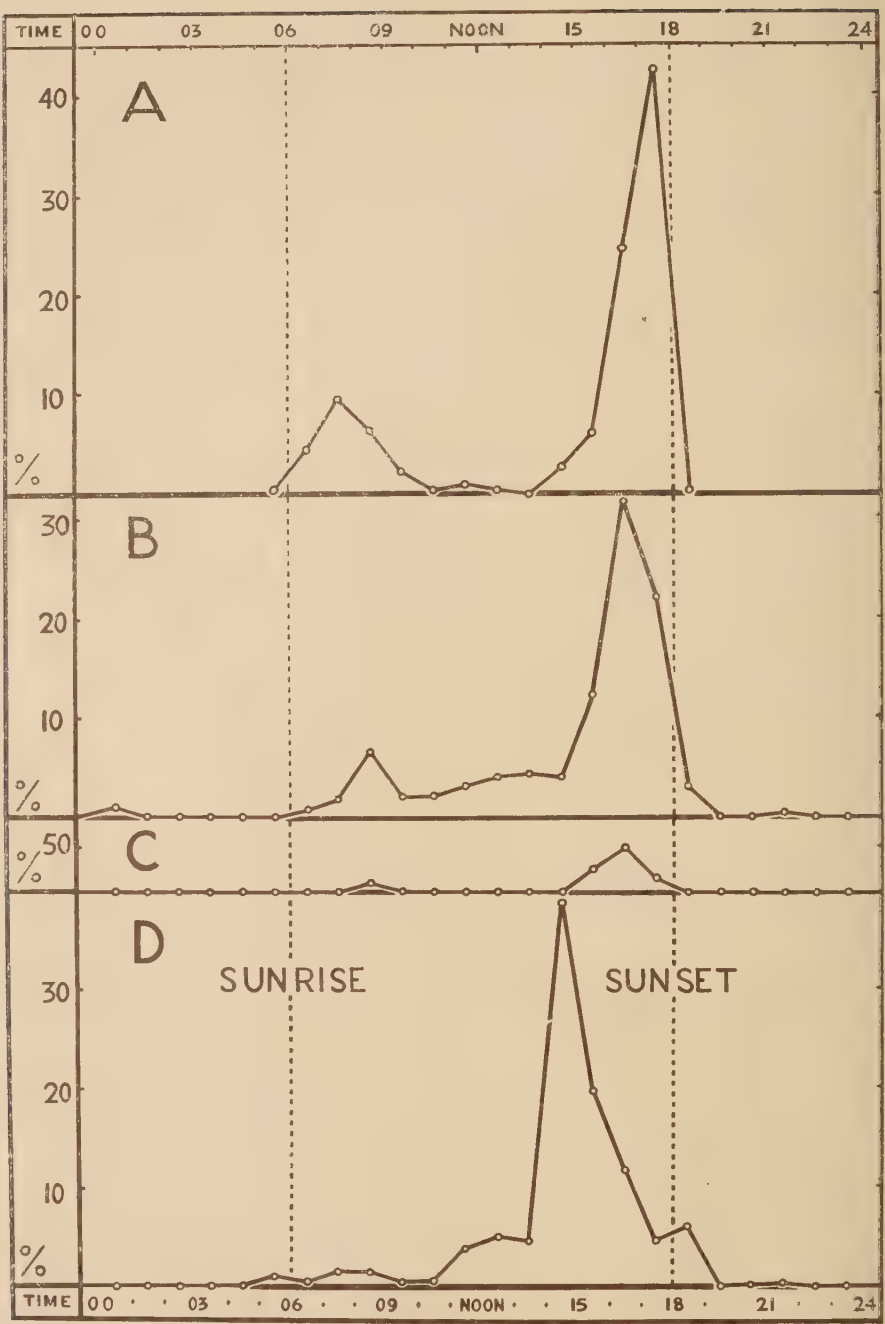


Fig. 1.—(A) Flight activity of males and females of *Aëdes aegypti* at Bunono, near Entebbe, Uganda. Smoothed geometric means on an hourly basis calculated from thrice-hourly observations from 0550 to 1810 hr. on three days. Figures reduced to a percentage basis to facilitate comparison. (B) Biting activity of *A. aegypti* at Bunono. Geometric means of hourly incidence of females on catching team in ten 24-hour catches. Figures reduced to a percentage basis. (C) Incidence of males of *A. aegypti* on catching team in the above series of 24-hour catches. The curve has been drawn on a reduced scale so that the numerical relationship between the incidence of males and females is preserved. A given height on curves B and C therefore represents the same mean incidence per hour. (D) Oviposition cycle of *A. aegypti* (after Haddow & Gillett, 1957).

females plotted in fig. 1B. Almost two-thirds (66%) of the biting activity occurs in the three hours before sunset, with a well-defined peak in hour 16–17, the only hour in which *A. aegypti* never failed to bite. A small morning peak, comprising 7 per cent. of the total, occurs in the third hour after sunrise. These

TABLE III.

Totals and geometric means of estimated numbers of *A. aegypti* in flight at 20-minute intervals between 0550 and 1810 hr. on 3 consecutive days.

Time	Total no.	No. of days	Running $M_G \times 100$	Hourly means	h.m. as %
0550	1	1	25		
0610	4	2	54		
30	2	1	80	64	4·5
50	5	2	58		
0710	1	1	104		
30	7	3	143	136	9·5
50	10	3	162		
0810	2	2	119		
30	3	2	79	92	6·3
50	4	2	79		
0910	2	2	59		
30	1	1	26	31	2·2
50	0	0	8		
1010	0	0	0		
30	0	0	0	5	0·4
50	0	0	16		
1110	2	2	16		
30	0	0	16	13	0·9
50	0	0	8		
1210	1	1	8		
30	0	0	8	5	0·4
50	0	0	0		
1310	0	0	0		
30	0	0	0	0	0·0
50	0	0	0		
1410	0	0	8		
30	1	1	39	37	2·6
50	5	2	63		
1510	2	2	70		
30	2	1	69	87	6·1
50	4	2	122		
1610	8	3	202		
30	12	2	351	351	24·6
50	18	3	500		
1710	23	3	749		
30	29	3	732	608	42·6
50	17	3	342		
1810	1	1	26		

four hours, moreover, are the only ones in which males were taken alighting on the bait, with a peak also in hour 16–17 (fig. 1C). The remaining hours of daylight account for 23 per cent., the hour immediately after sunset, and probably only early in this hour, 3 per cent. Truly nocturnal activity is only 1 per cent. of the total, and is thus not significant.

Flight activity.

The figures are given in Table III, and the hourly geometric means on a percentage basis plotted in fig. 1A. The morning and afternoon peaks are even more sharply defined than in the biting cycle, but bear a similar ratio to each other. The ratio of the morning peak to the afternoon peak is 1:4·5 (flight activity) and 1:4·8 (biting activity). The morning peak occurs in the second hour after sunrise, one hour earlier than in the biting cycle; the afternoon peak one hour later in the hour before sunset. If the afternoon biting peak is calculated only from the 72-hour catch, it coincides with the contemporaneous flight-activity peak.

Swarming of males and females, as defined above (p. 228), was observed during the peak period of flight activity from 1630 to 1750 hr., on two days out of the three. On the day before these observations, also, swarming was noticed at this time, and a male and female were seen to leave the swarm and copulate on the tip of a grass leaf. Swarming occurred in the same spatial location on each of the three occasions, about one foot above a metal platform, on which the tyres rested, between the piles of tyres and some overhanging elephant grass.

Discussion and Conclusions.

Teesdale (1955) published arithmetic totals only for his series of 24-hour catches near Mombasa, on the Kenya coast. He has subsequently (Teesdale: personal communication) calculated geometric means, which, however, show no important differences. In all his catches, both morning and afternoon activity peaks were present. It is important to notice that a sharp peak confined to a single hour may not indicate such high activity as lower values spread over several hours. In three series of catches, he found that inside a house and also outside (but near houses) most biting occurred in the morning; outside, the afternoon peak (confined to the single hour before sunset) reached the highest hour value. In a plantation away from houses most biting occurred in the afternoon, with a peak in the hour before sunset.

Teesdale also made a long series of diurnal biting catches in the plantations and found a biting peak in the hour after sunset. Since less than half his catches included this hour, the evidence of a crepuscular peak cannot be regarded as reliable. The general form of his curve is the same as that for his 24-hour plantation catch.

Van Someren, Heisch & Furlong (1958) carried out a very similar series of catches at Ganda, about 60 miles northwards along the coast from Mombasa. Comparison of their figures with those of Teesdale shows no evident differences for inside and outside houses and in the plantations, except that outside but near the houses their afternoon peak is less marked.

The present study can thus be reconciled with the plantation catches of Teesdale and van Someren, Heisch & Furlong, but not with the catches inside and near houses.

Mattingly (1957), summarising the evidence on the relative domesticity of the three forms of *A. aegypti* on the Kenya coast, concludes that var. *queenslandensis* (Theo.) is wholly domestic, the subspecies *formosus* entirely wild, and the type form intermediate. In neither Teesdale's nor the catches of van Someren, Heisch & Furlong was any separation between the forms made, but

the latter authors state that in the plantations ssp. *formosus* is the form mainly encountered, and var. *queenslandensis* inside houses. Of a large series of *A. aegypti* obtained in the plantations by the present author and submitted to Mrs. van Someren, the majority were ssp. *formosus*. The statement by Mattingly (1957) that Teesdale may be supposed to be dealing wholly or in part with the type form outside may be true for the catches near houses, but in the plantation it seems that his catches (in which most biting occurred in the afternoon, with a peak in the hour before sunset) would have been mainly of ssp. *formosus*, unless the Mombasa area is different from Ganda.

From the well-defined biting cycle of *A. aegypti*, mainly ssp. *formosus*, at Entebbe, with a minor morning, and a major afternoon, peak (indicated also in the population in the Kenya coastal plantations, which, it is suggested above, would have been mainly of ssp. *formosus*) it seems justifiable to conclude that this typifies the biting cycle of ssp. *formosus* out of doors in both areas. Mrs. van Someren (personal communication) is able to confirm this from Ngong, near Nairobi. In five diurnal catches from 06 to 19 hr. in which she obtained 328 examples of *A. aegypti*, she recorded a biting-activity curve almost identical to that from Bunono.

Lumsden (1957) in Newala, southern Tanganyika, was almost certainly dealing mostly with a population of var. *queenslandensis* inside a hut and on a hut verandah (Mattingly, 1957). His results are difficult to reconcile with the inside and outside house catches on the Kenya coast, and since the present paper is concerned with the biting cycle of ssp. *formosus* away from the immediate vicinity of houses, detailed discussion of his work is probably outside its scope.

The close correspondence between the curves of biting activity and flight activity has already been noted above. This type of curve is seen again in the oviposition cycle of a laboratory colony of *A. aegypti* (Haddow & Gillett, 1957), and has been reproduced here in fig. 1D. The mosquitos used by Haddow & Gillett for these experiments would appear to have included both ssp. *formosus* and the type form, although the original stock included var. *queenslandensis*. The main oviposition peak is four hours before sunset, two hours earlier than the Entebbe biting peak, and there is a sign of a very small peak corresponding perhaps with the minor morning biting peak. This small peak, in the second and third hour after sunrise shows more clearly in three out of ten day-to-day figures, for normal daylight, and artificially reversed " night " and " day ".

It thus appears that, in respect of ssp. *formosus* at least, *A. aegypti* shows cyclical activity paralleling that of the closely related forest mosquito, *A. africanus*. This species has a single sharp crepuscular biting peak (Haddow, Gillett & Highton, 1947), and a sharp oviposition peak between one and two hours before sunset. Morning flight activity, not connected with oviposition, was observed in this species in the laboratory (Gillett & Haddow, 1957). The existence of a similar interval of two hours between oviposition and biting peaks in these two closely related species may be of help in elucidating the mechanisms underlying their basic activity rhythm. That ssp. *formosus* is the form of *A. aegypti* which in its habits approaches most closely to the wild sylvan species, *A. africanus*, lends support to the idea that the apparent lack of a similar cycle in var. *queenslandensis*, and perhaps in the type form, may be connected with its domesticity.

Further work on the Kenya coast, involving study of the three forms of *A. aegypti* separately, with emphasis on var. *queenslandensis* and the type form, seems necessary for at least an adequate understanding to be obtained of cyclical biting behaviour in the species as a whole.

Summary.

In an outdoor population of *Aëdes* (*Stegomyia*) *aegypti* (L.), mainly consisting of subsp. *formosus* (Wlk.), in Uganda, a series of ten 24-hour catches has shown

a sharply-defined biting cycle which corresponds closely to an observed diurnal cycle of flight activity. A main peak of activity occurs one or two hours before sunset, and a lesser peak two or three hours after sunrise.

Comparison with recent work in Kenya suggests that, in comparing the behaviour of populations out of doors with those indoors, a distinction must be made between ssp. *formosus* and the other two forms of *A. aegypti*, in which no similar cycle has yet been demonstrated.

Ssp. *formosus*, which is presumed to be the wildest form of *A. aegypti*, is shown to have a cyclical behaviour very similar to a related forest species. *A. africanus* (Theo.).

Acknowledgements.

The work of which this study forms a part is wholly financed by the Colonial Development and Welfare Fund. I am indebted to Dr. A. J. Haddow, Dr. W. H. R. Lumsden and Dr. J. D. Gillett for their valuable guidance and discussion. I have profited from discussions with Mrs. E. C. C. van Someren, Dr. C. Teesdale and Dr. P. S. Corbet, and thank the first two for allowing me to use their unpublished results. Mrs. van Someren kindly examined some of my material. The field work would have been difficult if not impossible without the assistance of Mr. Yovani Senkubuge and his catching team.

References.

Gillett, J. D. & Haddow, A. J. (1957). Laboratory observations on the oviposition-cycle in the mosquito *Aëdes* (*Stegomyia*) *africanus* Theobald.—*Ann. trop. Med. Parasit.* **51** pp. 170–174.

Haddow, A. J. (1945). The mosquitoes of Bwamba County, Uganda. II. Biting activity with special reference to the influence of microclimate.—*Bull. ent. Res.* **36** pp. 33–73.

Haddow, A. J. (1954). Studies of the biting-habits of African mosquitoes. An appraisal of methods employed, with special reference to the twenty-four-hour catch.—*Bull. ent. Res.* **45** pp. 199–242.

Haddow, A. J. & Gillett, J. D. (1957). Observations on the oviposition-cycle of *Aëdes* (*Stegomyia*) *aegypti* (Linnaeus).—*Ann. trop. Med. Parasit.* **51** pp. 159–169.

Haddow, A. J., Gillett, J. D. & Highton, R. B. (1947). The mosquitoes of Bwamba County, Uganda. V. The vertical distribution and biting-cycle of mosquitoes in rain-forest, with further observations on microclimate.—*Bull. ent. Res.* **37** pp. 301–330.

Haddow, A. J. & van Someren, E. C. C. (1950). A new species of *Stegomyia* Theobald from the Ruwenzori Range, Uganda.—*Ann. trop. Med. Parasit.* **44** pp. 281–284.

Lumsden, W. H. R. (1952). The crepuscular biting activity of insects in the forest canopy in Bwamba, Uganda. A study in relation to the sylvan epidemiology of yellow fever.—*Bull. ent. Res.* **42** pp. 721–760.

Lumsden, W. H. R. (1957). The activity cycle of domestic *Aëdes* (*Stegomyia*) *aegypti* (L.) (Dipt., Culicid.) in Southern Province, Tanganyika.—*Bull. ent. Res.* **48** pp. 769–782.

Mattingly, P. F. (1949). Studies on West African forest mosquitos. Part I. The seasonal distribution, biting cycle and vertical distribution of four of the principal species.—*Bull. ent. Res.* **40** pp. 149–168.

MATTINGLY, P. F. (1957). Genetical aspects of the *Aëdes aegypti* problem. I. Taxonomy and bionomics.—*Ann. trop. Med. Parasit.* **51** pp. 392–408.

VAN SOMEREN, E. C. C., HEISCH, R. B. & FURLONG, M. (1958). Observations on the behaviour of some mosquitos of the Kenya coast.—*Bull. ent. Res.* **49** pp. 643–660.

TEESDALE, C. (1955). Studies on the bionomics of *Aëdes aegypti* (L.) in its natural habitat in a coastal region of Kenya.—*Bull. ent. Res.* **46** pp. 711–742.

WILLIAMS, C. B. (1937). The use of logarithms in the interpretation of certain entomological problems.—*Ann. appl. Biol.* **24** pp. 404–414.

© Commonwealth Agricultural Bureaux, 1959.

THE BIOLOGY OF *NAUSIBIUS CLAVICORNIS* (KUG.) (COL., CUCUJIDAE).

By M. H. Breese and Thelma E. Wise

The Imperial College of Tropical Agriculture, Trinidad, The West Indies.

Nausibius clavicornis (Kug.) may be found in Trinidad in the bulk or bag stores of most sugar factories, and in wholesalers' warehouses. Populations are usually small and its presence had not attracted particular attention until 1954, when an experiment conducted at one factory to investigate the deterioration of raw sugar during storage became infested with it and with *Carpophilus obsoletus* Erichs. In this experiment, which was set up in mid-May 1954, two grades of unwashed sugar having sucrose contents of 97·8 and 95·8 per cent. and moisture contents of 0·5 and 0·8 per cent., respectively, were stored in each of the following ways:

(a) in 24 lagged, 2-gallon galvanised buckets each containing between 11 lb. and 13 lb. sugar,
(b) in six 250-lb. bags stacked three high,
(c) in two wooden boxes measuring 2 ft. 6 in. square by 4 ft. deep each containing about 900 lb. of sugar.

By mid-July the surface of the sugar in the buckets was covered with fungi as were the exposed parts of the stacked bags. A month later, molasses was settling in the bottom of the buckets and also running out of the bottom bags in the stack. Fungi were still very much in evidence on the sugar in the buckets but appeared to be less on the bags. By mid-September the fungi had disappeared but beetles were noticed in all types of storage. The infestation was investigated by the writers in early November 1954 by which time both *N. clavicornis* and *C. obsoletus* were abundant, the former considerably more so than the latter. Because of the infestation and of the serious deterioration in the condition of the sugar which had taken place in both the buckets and bags, the experiments with these forms of storage were terminated at the beginning of December 1954, and that with sugar stored in boxes in early January 1955. One of the buckets was brought to Imperial College and it was hoped that it would provide a stock of *N. clavicornis*, but after nine weeks the sugar had become so wet that only the periphery of its surface (comprising about one quarter of the surface area) showed any dry crystals. A few beetles had been drowned in the syrup and others had their bodies so covered with it that they were almost unable to move. It was considered that little further use could be made of the sugar as it stood, and all adults and larvae that could be found in it were therefore collected and transferred to cultures on Haydak's formula (see below). Larvae of *N. clavicornis* were found in the surface layer of even the wettest sugar, but pupae, which were few, only in the drier periphery where the pupal cells had been constructed just below the surface. Adults were also confined to this drier region or were congregated in folds of the sacking with which the bucket was lagged. No larvae of *C. obsoletus* were found and the number of adults of this species collected at "clearing" was only 14 as against 124 of *N. clavicornis*. It is possible that *C. obsoletus* was feeding on the moulds which at one time grew abundantly on the sugar, but that its numbers declined as the moulds disappeared.

There are several references to the occurrence of *N. clavicornis* in sugar, and according to Wolcott (1927, p. 221) it is occasionally a serious pest of brown sugar in Haiti. Patton (1931, p. 442), on the other hand, states that although it is a cosmopolitan species and common among ships' stores it is not a pest of

any importance. This author lists, in addition to sugar, the following commodities from which *N. clavicornis* has been recorded in Britain: rice, dried apples, ginger, logwood (*Haematoxylon*) and cassia husk. Wheeler (1921) quotes a number of United States records extending back to 1869, most of which include sugar among the products infested. Other commodities in which the beetle has been found in ships and storehouses in the U.S.A. are rice, " plant wares " and " other articles of commerce ". In the field, the beetle is said to occur under bark where it apparently feeds on sap. *N. clavicornis* has been found under decaying bark (of *Sapindus oahuensis*) in Hawaii (Anon., 1933), but it has not yet been found in such a situation in Trinidad, nor in any commodity other than sugar. Lepesme (1945, p. 137) quotes Fleutiaux as having reported it in various cereals in Guadeloupe, and Ganglbauer as stating that in South America it lives in old nests of bees.

In Europe, *N. clavicornis* occurs mainly in imported stored products, and Kugelann (1794) found his type specimen dead in a barrel in which cocoa beans had been stored.

Lepesme (*op. cit.*) states that it is rare in France and does not appear to be able to establish itself. He adds that " the life history of the larva is unknown, but it is unlikely that it is carnivorous; the larva probably lives, like the adult, on organic dried animal and more especially, dried vegetable matter."

In the West Indies there is considerable direct consumption of unrefined sugars, such as those known to the trade as " washed grey " and " yellow-crystal " sugar, which contain varying proportions of molasses. Washed grey is in effect a high quality raw sugar with a large crystal size, the higher quality having been obtained by washing off with water most of the molasses film from the sugar crystals during their centrifuging. Yellow-crystal sugar, which is generally called " brown " or " Demerara " sugar in Britain, is a very large-grained raw sugar to which reducing agents such as titanium chloride have been added during manufacture or centrifuging in order to give the molasses film on the crystals a golden-yellow colour. It is in these types of sugar that *N. clavicornis* is most commonly found in Trinidad, and in view of the possibility of its developing to pest proportions in them, investigations into its bionomics were undertaken.

Synonymy.

The genus *Nausibius* was erected by Redtenbacher (1858) on the basis of Marsham's *Corticaria dentata* (1802). The identical species had, however, been described earlier by Kugelann (1794) as *Cucujus clavicornis*. The synonymy as given by Blackwelder (1944–57), and probably taken from the Junk catalogue, is:

Nausibius clavicornis (Kugelann) (1794)

1802	*Corticaria dentata*	Marsham, T. Entomologia Britannica, sistens insecta Britanniae indigena, secundum methodum Linnaeanum disposita. 348 pp. London.
1850	*Silvanus latus*	Fairmaire, L. Essai sur les coléoptères de la Polynésie.—Rev. Mag. Zool. (2), **2** pp. 50–64.
1851	*S. intermedius*	Smith, F. List of the Coleopterous insects in the collection of the British Museum, part 1: Cucujidae, etc., pp. 1–25. London.
1858	*Rhyzophagus parallelus* ..	Walker, F. Characters of some apparently undescribed Ceylon insects.—Ann. Mag. nat. Hist. (3), **2** pp. 202–209.
1869	*Nausibius major*	Zimmermann, C. C. A. Synonymical notes on Coleoptera of the United States, with descriptions of new species, from the MSS of the late Dr. C. Zimmermann.—Trans. Amer. ent. Soc. **2** pp. 243–259.

Materials and Methods.

All experiments were carried out in desiccators containing a saturated solution of sodium chloride, placed in incubators at 85°F. (29·4°C.). At this temperature the relative humidity is controlled at almost exactly 75 per cent. (Carr & Harris, 1949). The desiccators were aerated each day with a stream of conditioned air. Stock cultures of the beetles were kept, both in the laboratory and at the controlled temperature and humidity, in 1-lb. jars containing a crumbled food material recommended by Haydak (1936) for the rearing of stored-products insects. The formula is as follows: Parts by weight: cornflour 4, whole-wheat flour 2, skim-milk powder 2, bran 2, dried powdered yeast 1. The dry ingredients are carefully mixed and then half the quantity by weight of a mixture of equal parts by volume of glycerine and honey is added. When all ingredients have been thoroughly mixed, using a pestle and mortar, they form a very thick paste which, after about 12 hours, sets to form a firm but easily crumbled food material. In oviposition experiments a slightly modified formula, which is discussed below, was used.

N. clavicornis is a difficult beetle to handle; it moves rapidly when disturbed, yet it retains a tenacious hold on any surface that offers a purchase and it resists determined efforts to dislodge it with a brush. Because of this and because most eggs are laid in, or on, the food, the method of recovering eggs from broken pieces of cork, as used by Thomas & Shepard (1940) with *Oryzaephilus surinamensis* (L.), is not suitable. It was found, however, that if the food rested on a perforated material lying directly against a dry surface, some eggs would be pushed through the perforations and would stick lightly to the surface below. Sufficient undamaged eggs for all experimental purposes were obtained, with little disturbance to the beetles, from "oviposition cylinders" (fig. 1) constructed as follows:

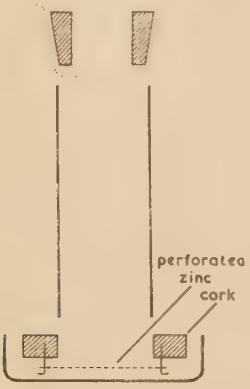


Fig. 1.—Oviposition cylinder.

the ends of a 2½ x 1 in. glass cylinder were ground flat, and a bored cork covered with muslin was inserted into one of these. The other end stood on a piece of thin perforated zinc (1 mm. perforations) which was held flush against the ground glass edge by being stapled to a square of ¼-in. cork sheet bored so as to fit tightly round the base of the cylinder. Cylinders were stood individually in small petri dishes and each contained five or six pairs of beetles and an adequate supply of food. Eggs were laid through the perforated zinc and stuck to the petri dish from which they could be recovered without damage.

In the study of the oviposition cycle, a washing and filtration technique was necessary for the recovery of eggs, and this involved using, in Haydak's formula,

ingredients that could be washed through a filter-disc of nylon net having 56 meshes to the inch. The same ingredients as in the basic formula were used, but the whole-wheat flour was sieved through nylon net as used for the filter-discs and the bran ground so as to pass through this net. The proportion of bran in the mixture was increased by 20 per cent. to allow for that sieved out of the whole-wheat flour and the proportion of whole-wheat flour was reduced accordingly. When soaked, some of the bran particles would swell and be retained on the filter disc, but never in such quantity as to interfere with the recovery of eggs.

For the investigation of the oviposition rate, pairs of beetles were confined with about 1 g. of modified Haydak's formula in 3 x 1 in. tubes closed with bored corks covered with small-mesh black nylon net. At the beginning of the oviposition cycle a small proportion of the eggs might be laid on the cork, and, to make these more easily visible, all bored corks used in oviposition tubes were dipped in black wax. A small piece of folded black paper was placed in each tube; this provided a resting place for the beetles and greatly facilitated their transfer from tube to tube. Eggs were counted at three-day intervals. After the transfer of the adults to new tubes, the food was covered with about 15 ml. of water and allowed to soak for one hour. Thereafter it was washed through the apparatus shown in fig. 2. The cut inverted bottle was used in exactly the same way as a three-piece

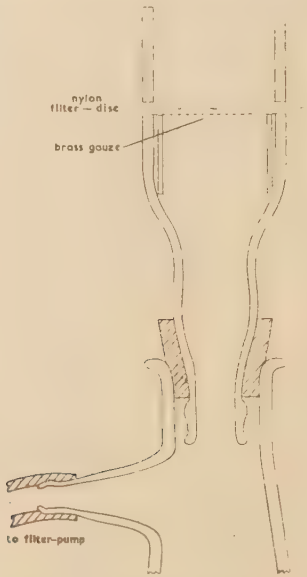


Fig. 2.—Filter apparatus for the recovery of eggs.

Buchner funnel, the nylon filter-disc being held between the ground edges and supported by a disc of medium mesh brass gauze which fitted inside the lower part of the funnel and rested on a glass cylinder inserted in this section. No damage to the eggs resulted from washing and filtration and recovery was excellent. The nylon discs were examined under the low power of a binocular microscope and eggs transferred to " solid " watch glasses (to record viability) on the tip of a moistened fine camel-hair brush.

The method of Thomas & Shepard (*op. cit.*) was followed in studying the incubation period and also the development of the larva. Eggs were placed individually, with a moistened camel-hair brush, just above the food supply on

the inner walls of 5-cc. vials containing about 0·5 g. of conditioned food material and closed with cotton-wool plugs. The vials were examined daily for hatchings of eggs and for moults. A moult was only recorded when the cast skin could be seen and removed.

Description of Stages.

Egg.

The egg is elongate-ovoid, average measurements being 0·84 mm. long by 0·26 mm. broad, and the colour is a shiny translucent white. The colleterial secretion which covers the chorion gives it a minutely rugose surface. At the anterior end of the egg this secretion hardens to form one, or more often two, short "tails". Eggs may be deformed by adherence to their neighbours or to the surface on which they are laid. Thus many have a narrow longitudinal flattening or even a slight concavity.

The light brown lateral ocelli of the embryo can be seen through the shell and are first apparent at a point three-quarters of the way along the egg from the posterior end. As in *O. surinamensis* (Back & Cotton, 1926), the fully developed embryo nearly fills the egg-shell, which becomes wrinkled and undulates with the movements of the embryo.

Larva (fig. 3).

Böving (1921), who divided the CUCUJIDAE into four families on the basis of larval characters, has given very full descriptions of the larvae of *Coccidotrophus socialis* (Schwarz & Barber) and *Eunausibius wheeleri* (Schwarz & Barber), which he placed in the family SILVANIDAE together with the genera *Oryzaephilus* Gangl., *Silvanus* Latr., *Nausibius* Redt., *Cathartus* Reiche and *Telephanus* Erichs. Silvanid larvae are without cerci; the eighth abdominal segment is normally developed, the ninth small and ventrally rudimentary, and the tenth is long and extends far behind the ninth segment.

The genus *Telephanus* is placed alone in the subfamily TELEPHANINAE whereas the remaining genera constitute the subfamily SILVANINAE. Larvae of the SILVANINAE have six ocelli in two distinct groups and the second antennal segment is large and clavate, the third segment very small or wanting. According to Böving, larvae of the genera comprising this subfamily "differ from each other only in small details such as the proportional length of the second antennal segment, the arrangement of the individual ocelli in the two ocellar groups, the thickness and colour of the chitin of the body or the number and development of the tergal setae".

Larvae of the genus *Nausibius* are distinguished by the mandible being "apically quadrifid; individual ocelli in each group are well separated and the body is well chitinised with dark brown chitinised shields".

In the larva of *N. clavicornis* the antenna is 3-segmented, the terminal segment being very small. The second antennal segment is more than twice as long as the basal segment and almost seven times as long as the terminal segment. The ratio of the length of the second antennal segment to the length of the head (from the tip of the labrum to the occipital foramen) is almost exactly 1 : 2.

There are four ocelli in the upper group and two in the lower. The upper ocelli form a trapezium with only the basal pair being separated from each other by more than half the diameter of a single ocellus. The lowest ocellus in the upper group is separated from the nearest one in the lower group by approximately two diameters.

The colour of the sclerotised parts of the integument is a mottled grey-brown, the head capsule and the terga of the fifth to eighth abdominal segments often being slightly darker. The frontal suture is lyriform and distinct, and a longitudinal line of weakness, along which the integument will split at ecdysis, runs

prominently down the middle of the thoracic terga. In each tergum except those in the ninth and tenth abdominal segments, a more lightly sclerotised pre- and post-tergal area can be distinguished. The pre-tergal area is cut off by a distinct line which, in all but the prothoracic segment, extends between short, nearly

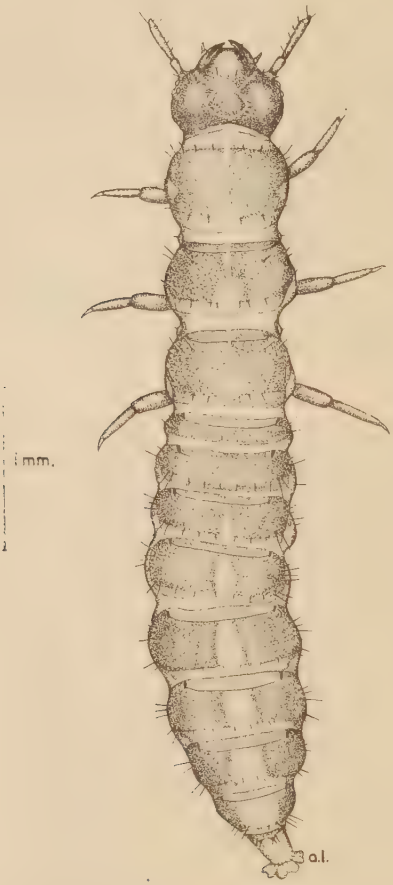


Fig. 3.—*N. clavicornis*, full-grown larva, slightly contracted: a.l., anal lobes.

parallel, antero-lateral black marks. The anterior margin of the post-tergal area is marked by six equally spaced, short, fine, recumbent bristles. The frons of the head capsule and the terga proper are sparsely set with minute setae. Near the lateral margins, the thoracic terga bear three, and the abdominal terga four or five, medium-length, erect bristles.

An ochreous area, which increases in size in successive segments, may be found centrally in the terga of abdominal segments 3 to 8. In some larvae, however, this area is distinct only in the 5th to 8th segments. There is a pair of minute papillae, each of which bears two short setae, on the posterior margin of the 9th abdominal tergum. The extrusible, membranous anal lobes are well developed (fig. 3, a.l.) and form adhesive pads which are used when the larva moves over smooth surfaces.

The average length of a full-grown larva is 5·5 mm. Earlier-stage larvae do not differ from the last instar except in size and in the form of the antennae, the second segment of which is almost pyriform in the first instar, but becomes more slender with successive moults.

Pupa (fig. 4).

Except for its larger size, the pupa is very similar to that of *O. surinamensis*. The skin of the last larval instar is not shed completely, but remains enveloping the terminal segments of the abdomen and conceals the characters by which the sex of the pupa can be determined. In a female pupa, two minute papillae are

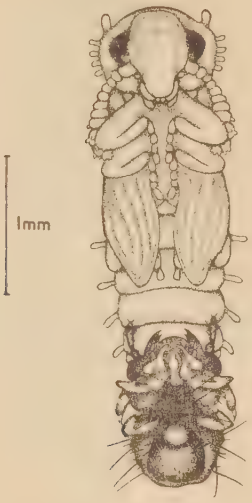


Fig. 4.—*N. clavicornis*, pupa.

found on the last abdominal segment, ventral to and very slightly in front of the urogomphi.

The newly formed pupa is shining white and totally devoid of pigmentation even in the eye facets.

Adult (fig. 5).

Redtenbacher (1858), who erected the genus *Nausibius*, defined it as in the following translation: "Antenna eleven segmented; segments close together, thickened and claviform from the eighth onwards, last segment triangularly tapered. Eyes large, strongly protruding, hemispherical. Mouthparts almost as in *Silvanus*, the inner margin of the mandible being only slightly excavate, with a very blunt tooth below the tip; first segment of the maxillary palp as thick as the following segments; labium broader than *Silvanus*, wider anteriorly and distinctly excavate at the tip. Abdomen and legs also as in the previous genus [*Silvanus*]; hind femora with a large, pointed tooth in the middle. The prothorax bears six strongly rounded tooth-like projections on each side."

In his original description of *Cucujus clavicornis*, Kugelann (1794) wrote (translation) "size, form and antennae as in the foregoing [*i.e.*, *Pediacus* (*Cucujus*) *dermestoides* (F.)], head and prothorax very dark brown, almost black, the latter generally quadrate, having several depressions centrally and five teeth

on each side. The elytra are somewhat lighter in colour and on each there are three slightly raised smooth lines and also some finely punctate lines."

A rather more accurate description is given by Redtenbacher (*op. cit.*): "Length 2/12 in., blackish-brown or red-brown, clothed with short, fine yellow-grey hairs; legs rust-red. Head triangular, with raised lateral margins, rather



Fig. 5.—*N. clavicornis*, ♂.

less densely punctate than the prothorax—the latter longer than broad, broadly rounded towards the scutellum, extremely densely punctate dorsally, with three indistinct, raised longitudinal lines and two depressions situated close together centrally in front of the posterior margin. Elytra slightly more than twice as long as their combined width, slightly broader than the prothorax, deeply excavate anteriorly, with prominent rounded shoulders and straight parallel sides; dorsally with narrow lines of dense punctures, alternating interstices being somewhat raised particularly towards the outside."

The foregoing descriptions are adequate except in reference to the elytra. These are marked with longitudinal lines of fine punctures which alternate with lines of close, rounded, though somewhat irregular depressions. There is a pair of punctures near the anterior border of each depression and the positions of the paired and single punctures are staggered. The golden-yellow recumbent bristles arising from the single punctures lie longitudinally, but those arising from the paired punctures diverge posteriorly. Alternate lines of single punctures are slightly raised, especially anteriorly, and in consequence, each elytron has four ridges the outermost of which is the most distinct as it lies along the angle between the horizontal, dorsal part of the elytron and the steeply sloping side.

Under normal top lighting, details of the punctation are obscured by the shining recumbent bristles, and the surface of the elytra appears "delicately reticulate" as described by Marsham (1802, p. 108).

The tooth on the posterior border of the hind femur is found only in the male. Males are slightly larger than the females, average measurements being 3·86 and 3·62 mm.

The morphology of the male genitalia of *N. clavicornis* and the wing venation have been described by Wilson (1930).

Pairing and Oviposition.

Pairing.

Copulation can take place within 24 hours of the emergence of either sex and it normally occurs almost immediately the unpaired sexes are put together. Subsequent copulations are thought to be infrequent; rarely were individual pairs observed *in copula* after the initial pairing, and in stock cultures copulating pairs were not often seen.

Oviposition.

There is a tendency for females to oviposit where eggs have already been laid, regardless of whether or not those eggs are their own. This is not necessarily a matter of a favourable site, because, in culture jars, clusters accounting for more eggs than a single female could lay in a given time were occasionally found on the gauze covering of the jar, *i.e.*, far from the food material. Similarly, where single pairs were confined in 3 × 1 in. tubes, the whole egg-production over a three-day period might be laid between the cork and its nylon covering. Normally, as stated above, eggs are laid in dry situations in or near the food, and clusters formed in cultures may be very large, containing between 30 and 40 eggs. Eggs adhere lightly to the surface on which they are laid, but more strongly to each other. Thus groups of up to five eggs laid by an individual female would occasionally remain intact throughout the washing and filtering process. In the study of the oviposition cycle, it was found that in the early stages most females would tend to lay some of their eggs against the nylon-covered cork of the 3 × 1 in. tube, but this tendency did not usually persist beyond the fourth week after the beginning of laying. A few, however, persistently laid some eggs on the cork for more than seven weeks before confining the whole of their oviposition to the food. Once abandoned, oviposition on the cork was rarely resumed and, if so, seldom for more than two 3-day laying periods. Because eggs were removed every three days they could not provide an oviposition stimulus for longer than this period, but it is possible that part of the colleterial secretion remains and induces a female to lay in situations other than those close to the food, especially during what might be termed the exploration period of the oviposition cycle.

The time-consuming nature of the filtration method of recovering eggs limited the number of beetles that could be used in the study of oviposition. Three series, each of six pairs of beetles, were set up on the modified Haydak's formula. In individual pairs the sexes were approximately the same age, but no female was more than ten days old. Males were present throughout; if a male died it was replaced by another of about the same age. The average length of life of a female was 99 days but there were considerable differences in the life spans of individual females (Table I) and in the total number of eggs laid (Table II).

TABLE I.

Length of life of ovipositing females kept on Haydak's formula.

Days	0–20	21–40	41–60	61–80	81–100	101–120	121–140	141–160	161–180
No. of ♀♀	1	1	0	3	5	2	1	3	1

TABLE II.

Total number of eggs laid by females kept on Haydak's formula.

Total no. of eggs	<50	51–100	101–150	151–200	201–250	251–300	301–350	351–400	401–450	451–500	>500
No. of ♀♀ ..	2	0	2	0	3	3	2	2	1	1	1

One ♀ escaped.

The shortest life was 17 days in a female that laid 32 eggs, the longest, 163 days in a female that laid 595 eggs. One female lived 40 days but laid only one egg in this time. The average number of eggs laid was 275. The oviposition cycles of the three series showed, however, only small differences and all results have therefore been combined to give fig. 6. Deaths occurred at almost regular intervals during

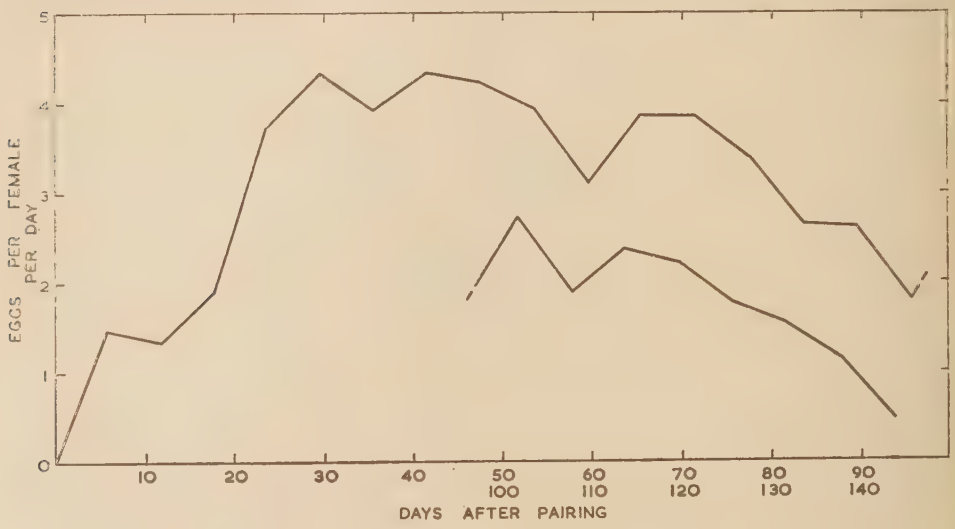


Fig. 6.—Average oviposition rate of *N. clavicornis* (eggs/♀/day) when males are present throughout life. (Average is for females alive at time of laying.)

the period of the experiment and the graph shows the average oviposition rate of a diminishing number of females.

Although copulation may take place within 24 hours of emergence, eggs are not normally laid until females are four or more days old. The maximum oviposition rate is reached in about 30 days. Pairing the female shortly after emergence appeared to depress the initial oviposition rate (see fig. 7), and although the maximum rate would be reached in approximately the same time, during the first 30 days of the oviposition period the proportion of the total number of eggs laid was significantly lower when females were paired within 24 hours of emergence than when they were allowed a maturation period of at least four days.

The fall-off in egg production at the end of the oviposition cycle is usually sharp, and only in the long-lived females (120 days or more) did the oviposition rate show any gradual decline. The post-oviposition period varied between less

than three and more than 21 days but most females (12 out of 17) died within nine days of finishing laying.

The highest number of eggs laid by any female in these series in a 3-day period was 26, but when eggs were recovered daily from five individual females of unknown age (with males) taken at random from stock cultures, as many as

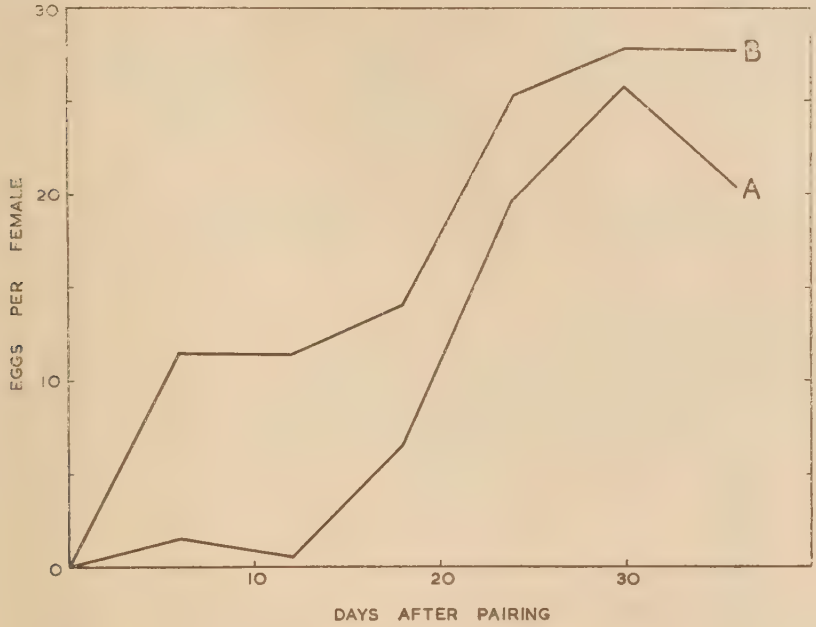


Fig. 7.—Difference in the initial oviposition rate (eggs/♀/6-day period): A, females paired within 24 hours of emergence; B, females paired when four or more days old.

12 eggs were laid in a 24-hour period. The daily egg production over ten days of these five females (Table III) suggests that changing the food each day may have stimulated increased oviposition.

TABLE III.

Daily oviposition of 5 individual females (with males) taken at random from stock cultures (on Haydak's formula).

Female no.	Day										10-day total
	3*	4	5	6	7	8	9	10	11	12	
1 ..	4	4	6	11	3	0	3	4	3	6	44
2 ..	7	6	5	6	12	6	5	6	6	6	65
3 ..	0	9	0	12	6	12	6	12	5	11	73
4 ..	6	1	0	6	6	5	5	6	9	6	50
5 ..	10	6	11	5	4	6	5	9	9	8	73
Average	5·4	5·2	4·4	8·0	6·2	5·8	4·8	7·4	6·4	7·4	61

*Pairs allowed one day to settle down, first egg count was made on second day, but was not recorded.

Viability.

The viability of eggs laid by females that had males present throughout life varied between 68 and 94 per cent., the overall viability being 85 per cent. No eggs were laid by virgin females. Females, separated from males immediately after laying the first egg, laid a proportion of viable eggs throughout the oviposition cycle, and in a cycle extending over 92 days after the removal of the male the most productive female laid 262 eggs of which 84 per cent. hatched. Experiments, not sufficiently replicated for statistical analysis, indicated that with a single copulation the duration of the cycle, the number of eggs laid and the viability are all reduced, but that even after about 90 days a second copulation will stimulate a marked increase in oviposition and raise the viability.

Incubation.

The incubation period varied between two and six days with 54 per cent. of the eggs hatching in five days. The average incubation period, based on 125 eggs, is 4·86 days.

Post-oval Development.

In the study of the individual development of 66 larvae it was found that approximately half (56 per cent.) underwent six moults and the remainder five moults. The frequency distribution histogram (fig. 8) of the head-capsule widths

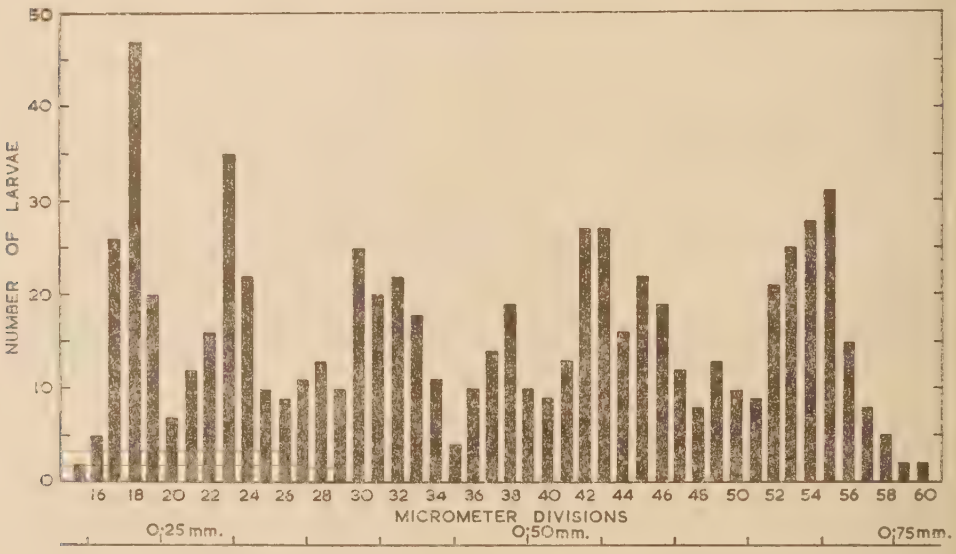


Fig. 8.—Frequency distribution histogram of the head-capsule widths of larvae taken at random from cultures.

of larvae taken at random from cultures also indicated that populations are normally made up of individuals having five or six larval instars. The numbers of males and females having five or six larval instars when the development of 15 larvae was studied and when great care was taken not to disturb them in the removal of the cast skins are shown in Table IV.

The probability of the distribution of this Table is 0·03 and although the number of adults is small there is a clear indication that where disturbance is minimised, females tend to have one more larval instar than males. Disturbance

generally results in both sexes having six larval instars and may, if severe, induce a seventh moult. Thirty adults were reared from larvae whose head-capsule widths were measured in the fourth and subsequent instars and the number of males and females having five, six and seven larval instars was as follows: five instars, 1 ♂, 1 ♀; six instars, 12 ♂♂, 13 ♀♀; seven instars, 1 ♂, 2 ♀♀.

TABLE IV.

Numbers of males and females having five or six larval instars.

Sex	Numbers having		Total
	Five instars	Six instars	
♂ ..	5	1	6
♀ ..	2	7	9
Total ..	7	8	15

The average duration of the instars in larvae having five and six instars, respectively, and the mean development period are shown in Table V. These larvae were not disturbed during development except in so far as was unavoidable in the removal of the cast skin.

TABLE V.

Duration of instars and mean development period (in days, on Haydak's formula) when the number of larval instars is five or six.

No. of larvae	No. of instars	Egg	Duration of instars							Mean development period
			I	II	III	IV	V	VI	Pupa	
29 ..	FIVE	(4·86)	4·59	3·86	2·72	3·00	6·24	—	5·00	29·97 ± 0·71
44 ..	SIX	(4·86)	4·11	3·68	3·41	3·32	2·70	5·84	4·66	32·30 ± 0·51

There is a significant difference of 2·33 days between the mean development period of adults having five and six larval instars, respectively. The variation in the total development period when the number of larval instars is five or six is shown in fig. 9. In the three instances where seven moults were induced the total development periods were 30, 33 and 38 days.

Larval mortality.

No experiments were run for the sole purpose of determining mortality in the larval and pupal stages. In the study of the number of larval instars in males and females, 9·5 per cent. of the larvae died; in the study of the post-oval development period, 8 per cent. of the larvae died; and when the head-capsule widths of larvae were measured in the fourth and subsequent instars—a procedure involving narcotisation—32 per cent. died. It may be presumed, therefore,

that when growing conditions are good, larval mortality on Haydak's formula, at 85°F. and 75 per cent. R.H., is low.

Feeding.

If undisturbed, a larva will often form a "feeding chamber" in the early instars and may utilise for this purpose any small crevice in the food material or

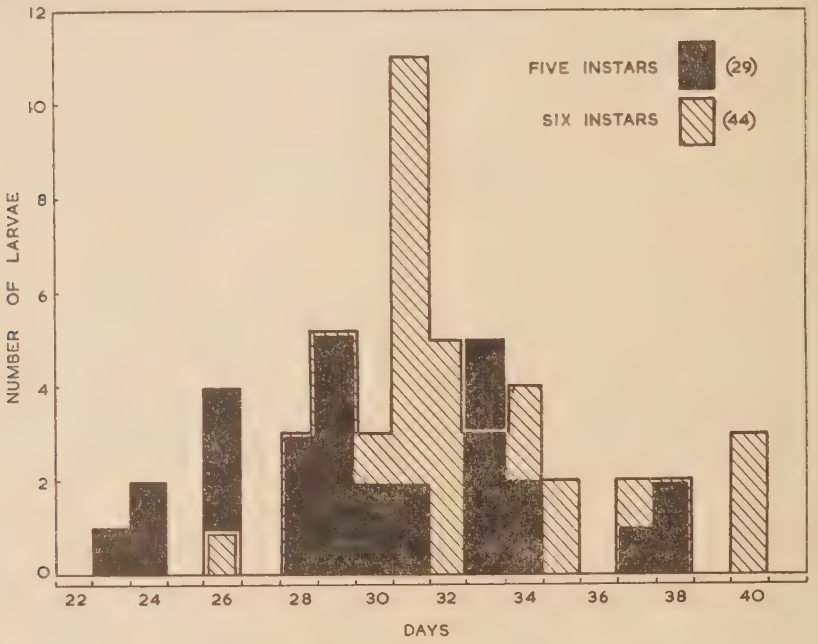


Fig. 9.—Variation in the total development period when number of larval instars is five or six.

a space between the food and the walls of the container. The chamber is enlarged by the feeding of the larva and frass is pushed out of it to form a loose periphery which is extended with the growth of the larva. Alternatively, the larva may make a shallow groove in the surface of the food and cover itself loosely with a mixture of frass and food particles. The presence of three or four exuviae close together at the periphery of individual chambers indicates that larvae may, unless disturbed, remain throughout development in these chambers.

Prepupa.

Soon after the last stadium is entered the construction of a pupal chamber is usually begun. If at this time the larva is occupying a feeding chamber, this may be used without particular alteration, but occasionally a special chamber is made by such larvae as well as by those that have hitherto moved about freely. About one day after its penultimate moult, the larva becomes shortened and consequently darker and it cements together frass and small particles of food over itself to form a loose covering. In this chamber, which is usually formed on the food material, the larva remains almost motionless for about two days, during which time it feeds very little. One or two days before pupation, the larva becomes cemented by its anal process to the substratum and feeding ceases entirely. The

body is supported by its elongate tenth segment and held parallel to the substratum, and the prepupa remains rigid and almost completely immobile in this position until pupation. A few larvae pupate nakedly on the surface of the food.

Pupa.

The age of the pupa can be determined by the degree of pigmentation and by movements of the distal parts of the limbs that take place during the latter half of the pupal period. About 24 hours after pupation the pigmentation of the eyes begins. The facets become light brown and can be made out individually. This pigmentation darkens progressively until on the third day the facets are quite black and are almost completely contiguous. At this stage in development the tarsal claws and the extreme tips of the mandibles become light brown, and shortly after the pigmentation of these parts first becomes discernible a vibration of the tarsal claws may be seen. As pigmentation spreads from the claws up the segments of the tarsi, so movement extends to these parts and this movement continues with only slight pauses until the emergence of the adult. During the fourth day, the tibiae and tips of the femora become light brown as also do the mouthparts, antennae, and the front of the head up to a line drawn between the bases of the antennae. On emergence, which usually takes place some time during the fifth day, all appendages are a light tan colour. The pigmentation of the head is lighter on the vertex and is abruptly lighter posterior to a line drawn across the head behind the eyes. Pigmentation is only just beginning in the elytra and sternites of a newly emerged adult.

Length of Life of Adults.

In cultures of single pairs that were kept under laboratory conditions specifically for the study of length of life, the average life of males and females was 223 and 174 days, respectively, with a maximum of 281 days in males and 224 days in females. The longest life recorded under controlled conditions was 209 days for a male and 163 days for a female (p. 246).

Life-history on Sugar.

Attempts were made to study the life-history of *N. clavicornis* on raw sugar, under controlled conditions, in the same way as had been done on Haydak's formula. Fresh raw sugar was obtained and kept in a muslin-covered jar for six weeks before being used. When used, the sugar had a sucrose content of 95·5 per cent. and a moisture content of 1·3 per cent.

Oviposition.

Two series of six pairs of beetles reared and matured on Haydak's formula were used. Pairs were of approximately the same age and the age of females at pairing varied between two and 14 days. There was, as in previous experiments, great variation in the length of life of females (Table VI), the average being 73 days as against 99 days on Haydak's formula.

TABLE VI.

Length of life of ovipositing females kept on sugar.

Days	0–20	21–40	41–60	61–80	81–100	101–120
No. of ♀♀	1	2	1	1	5	2

Oviposition was extremely poor, the greatest number of eggs laid by any female being 16. Four females laid no eggs at all. Of the eight females that laid one or more eggs, six had laid all within six days of pairing; another laid six out of a total of seven within three days of pairing, and the final egg, which was flaccid and infertile, between six and nine days later. Two females showed an interesting oviposition behaviour. One that lived for 86 days laid no eggs during the first 48 days after pairing and then four (her total egg production) during the next 3-day period. The second, which laid the highest total, of 16 eggs, laid one in the first three days after pairing, none for the next 45 days, then 15 during the next 15 days. This female lived for 20 days after laying her last egg.

The viability of the eggs that were laid shortly after the females had been paired and placed on sugar averaged 78·5 per cent. Of the four eggs that were laid by one female 48 days after pairing, two hatched, and of the 15 that were laid by another after an interval of 45 days, ten hatched. It may be presumed that the eggs laid shortly after pairing had matured while the beetles were on Haydak's formula, but it would appear that the sugar lacked some food factor or factors necessary for normal egg-production. Some measure of confirmation of this low egg-production on sugar was obtained with females collected or reared from infested sugar. An infestation, by *N. clavicornis* and *Oryzaephilus mercator* (Fauv.), was found in a small stack of yellow-crystal sugar in a factory store. Six individual pairs of beetles, of unknown age, from this infestation were placed each on 1 g. yellow-crystal sugar in 3 × 1 in. tubes. Egg counts were made after three days and then daily for ten days. The results are shown in Table VII. Daily disturbance appears here to have caused a reduction in the oviposition rate; this is the opposite of the effect shown when eggs were recovered daily from females on Haydak's formula (Table III).

TABLE VII.

Daily oviposition of 6 individual females (with males) taken at random from infested yellow-crystal sugar.

Female no.	Day											10-day total
	0–3	4	5	6	7	8	9	10	11	12	13	
1 ..	14	0	6	0	0	0	0	0	0	6	0	12
2 ..	2	0	0	0	0	0	2	0	0	0	0	2
3 ..	0	0	0	0	0	0	0	0	0	0	0	0
4 ..	4	0	0	0	0	0	0	0	0	0	0	0
5 ..	6	0	0	2	0	2	0	0	1	0	0	5
6 ..	5	0	0	7	0	6	0	0	1	0	0	14

The low egg-production was accompanied by a low viability. Many eggs were so fragile that it was impossible to remove them intact from the filter discs and, of a total of 64 laid, 25 were destroyed. Of the remaining 39 only 17 (43·6 per cent.) hatched.

Extremely low egg-production and viability were again recorded when the oviposition cycle of three females, reared on sugar, was studied. Three pairs of beetles were reared from larvae collected as prepupae from the infested yellow-crystal sugar. The females were between five and eight days old when paired with males of approximately the same age, and the pairs were provided throughout the experiment with sugar from the same sample as that on which they had been reared. One female died 92 days after pairing, having laid one egg, but the oviposition of the other two was studied for a further 33 days. The totals of eggs

laid by these females in 125 days were 7 and 3, of which 2 and 0, respectively, hatched.*

Larval development.

Attempts to rear adults from larvae kept individually on raw or yellow-crystal sugar were not successful. Most larvae died in the first instar on both types of sugar and only on yellow-crystal sugar did any larva develop to the pupal stage (Table VIII).

TABLE VIII.

Number of larvae dying in successive instars on raw and yellow-crystal sugar.

Instar in which larva died ..	I	II	III	IV	V	VI	Pupa	Total
Raw sugar	13	0	1	0	0	0	0	14
Yellow-crystal sugar	14	0	?1	2	2	0	1	20

The number of days a larva remained in the instar in which it died was often high. On raw sugar, of the 13 larvae that died in the first instar, five had been in this instar for more than nine days, and on yellow-crystal sugar two larvae died after 15 and 25 days, respectively, in the fourth instar and another died after 23 days in the fifth instar. The individual that died as a pupa had spent 15 days in the fifth (*i.e.*, last larval) instar. Up to the end of the third instar, however, the development of larvae that died in the later instars was not much slower than on Haydak's formula (see Table IX and *cf.* Table V). Lack of incubator space did not allow of the individual rearing of large numbers of larvae, by which means it might have been possible to discover if they could complete development despite long periods spent in one or more instars.

TABLE IX.

Duration of instars and length of life (in days) of larvae surviving up to the fourth or later instars on yellow-crystal sugar.

Larva	Instar							Length of life
	I	II	III	IV	V	VI	Pupa	
1	7	3	2	6	23	—	—	41
2	4	5	3	8	15	—	8	43
3	5	3	3	25	—	—	—	36
4	5	8	2	8	5	—	—	28
5	4	3	6	15	—	—	—	28
Average ..	5·0	4·4	3·2					

Some indication of the length of time that might be spent in the larval stage was, however, obtained when 30 first-instar larvae were placed together on about 5 g. of raw sugar. Three of these survived for between 88 and 93 days, when,

* After 125 days, the females were transferred to Haydak's formula and lived for a further 21 and 29 days, respectively. The one that had laid seven eggs on sugar laid a further eight, of which three hatched; the other, which had laid three eggs on sugar, laid a further 20, of which nine hatched.

from head-capsule measurements, they were considered to be in the fifth or sixth instar. After 88 days, when the larvae had apparently been in the one instar for at least two weeks, so much water had been absorbed by the sugar that no dry pupation sites were available. A little drier raw sugar was therefore added, but all larvae died within the next five days, having shown no sign of pupating.

Length of life on sugar.

Beetles, especially males, were able to survive for long periods on raw and yellow-crystal sugar and on the syrup to which these sugars would eventually be converted after prolonged exposure to a relative humidity of 75 per cent. The six pairs (see Table VII) that were collected on yellow-crystal sugar were kept after the termination of the daily oviposition study, without further change of sugar, until death. Five of the females lived for more than 80 days after collection and all the males lived for more than 100 days, two surviving for over 145 days. Syrup would " creep " up the folded black paper on which the beetles rested, confining the beetles eventually to the upper edge of the paper. Beetles would descend to the wetter part to feed, but in so far as could be judged from the microscopic examination of wet paper, no scarification occurred. Reference has already been made (p. 252) to females that were reared on yellow-crystal sugar and whose oviposition on this sugar was studied for 125 days.

Observations on a naturally occurring infestation.

The experiments conducted under controlled conditions with raw and yellow-crystal sugar indicate that although females might be long-lived, oviposition is very low and the viability of the eggs much lower than with females living on Haydak's formula. There is a high larval mortality especially in the early instars and slow development in those that reach the fifth or sixth instar.

These indications were endorsed by observations made on a naturally occurring infestation, to which reference has already been made (p. 252). This infestation was in a small stack of 16½ bags of yellow-crystal sugar which had been in store for seven months when first examined. After a further two months' storage the half-bag, containing 57 lb. of sugar, was brought to the laboratory for observation. Most of the sugar had a sucrose content of 94 per cent. and a moisture content of approximately 1 per cent., but at the surface (the bag had been standing vertically) the sucrose content was 92·8 per cent. and the moisture content approached 2 per cent. There was also a layer about 2 in. deep of wetter sugar (2 per cent.) near the bottom of the bag. Vertical cores and horizontal probe samples showed that the infestation was confined to the surface and peripheral sugar in the bag.

Adults and larvae were collected by sucking-tube over a period of ten days. Then, when no more could be found, the surface and peripheral sugar was carefully removed, dissolved, and washed in small quantities through nylon filter-discs. By collection and filtering, 121 adults and 91 larvae were obtained, but only one pupa and one egg were found. The head capsules of 45 of the larvae, selected at random, were measured, and the measurements indicated that most were in the last instar and that this instar was the sixth (Table X).

TABLE X.

Distribution of larvae within instars in a sample from a natural infestation, based on head-capsule measurements.

Probable instar ..	I	II	III	IV	V	VI
No. of larvae ..	1	1	2	5	6	30

Six larval instars assumed.

Provided that oviposition is normal and that there is no differential mortality in the different instars, the numbers of the various stages of the beetle occurring in any population are in proportion to the duration of those stages. Assuming six instars and a development similar to that on Haydak's formula (see Table V), the numbers of second-, third- and fourth-instar larvae would be approximately equal, there would be rather fewer fifth-instar larvae, and about twice as many sixth-instar as fifth-instar larvae. Even if allowance is made for the fact that there is always a proportion of the larger larvae that cannot be classed definitely as fifth- or sixth-instar on the basis of head-capsule measurements, it is clear that there is an unusual preponderance of larvae in the sixth instar and rather more in the fourth and fifth than would have been expected if development had been normal. This is in agreement with the experimental finding, on sugar, that the time spent in these instars is usually long, and that some larvae in the fourth and subsequent instars are unable to moult, and eventually die. Despite the low numbers of eggs obtained on sugar in experiments, more might have been expected from the surface and peripheral sugar that was dissolved and filtered, unless there was any tendency for eggs to be laid against, and to adhere to, the inside of the bag. Similarly, if pupae were formed against the sacking they would be difficult to detect and would not be recovered by filtration. Of the larvae collected, four pupated within seven days of the beginning of collection, indicating that they must have been on the point of pupation when removed from the bagged sugar. However, only two adults emerged from these pupae.

Discussion.

Haydak's formula is probably well suited to the nutritional requirements of *N. clavicornis* and on this food material the beetle develops rapidly and is capable of a high rate of oviposition. Taking the egg mortality at 15 per cent. and the larval mortality at 8 per cent., the weekly self-multiplicative rate (Howe, 1953) is 1·67. This is lower than that of *O. mercator* and a good deal lower than *O. surinamensis*, both of which have a shorter larval period and attain the peak of their egg-production more rapidly. Nevertheless, it is sufficiently high to suggest that on suitable commodities *N. clavicornis* might be a serious pest. Although its distribution is cosmopolitan, reports of its having become a pest are very rare, suggesting that most stored products in which other Cucujids are found are not attractive to *N. clavicornis* or are nutritionally deficient and do not provide for a rapid rate of multiplication. On the other hand the beetle has most frequently been reported from sugar, which in its highly pure refined form is unlikely to be a complete food. In Trinidad, the few adults found in refined sugar have undoubtedly been instances of cross-infestation, and proved cases of breeding have been confined to raw or yellow-crystal sugar. Larvae have, however, also been found in damp spillage of washed grey sugars and feeding on the syrup which often drips from the bottom bags of large stacks of such sugar after prolonged storage. In all unrefined sugars the crystals are coated with a thin film of molasses, but both the proportion of the molasses and its quality vary from grade to grade and within a grade. In general, however, the quantity of molasses adhering to the sugar crystal varies inversely with the sucrose content of the sugar sample. Molasses is the solution left after as much as is possible of the sucrose has been crystallised from the concentrated sap of the sugar-cane and therefore it contains most of the original constituents of the cane sap, together with residues of certain of the chemicals used in sugar manufacture. Thus, besides a high content of sucrose and invert sugars such as glucose and fructose, it also contains inorganic salts of both organic and inorganic acids and smaller amounts of a number of organic substances including amino acids, proteins and vitamins. This molasses film covering the sugar crystal is hygroscopic and takes

up water in humid climates. The effect of this dilution is to allow part of the sugar crystal to go into solution in its molasses film, but because the absorption of water takes place more rapidly than the sugar dissolves, the sucrose content at the surface of the film becomes sufficiently low for micro-organisms to establish themselves in it. Where continued water uptake can occur, deterioration is thenceforward progressive. The micro-organisms invert sucrose and ferment invert sugars; more sucrose goes into solution and with prolonged storage the syrup formed eventually oozes from the exposed bags even of washed sugars. In sugar manufacture, a low moisture content (below 1 per cent.) of the fresh product is aimed at and, in most factory stores, measures are taken to reduce water uptake as much as possible, but the presence of some syrup around the base of a stack is quite common.

Reference has already been made to the occurrence of *Oryzaephilus mercator* with *N. clavicornis* in yellow-crystal sugar and in a survey of factory stores it was usually found that, where sugar was infested at all, these two species tended to occur together. Although no quantitative estimation of infestations has been made, the presence of larvae as well as adults of *O. mercator* indicates that this Cucujid may also be able to breed in certain types of sugar.

Howe (1956) has shown the preference of *O. mercator* for oilseeds and their derivatives and that of *O. surinamensis* for starchy foods, but he does not indicate any differences in their preferences for sweet products with a high moisture content. Fraenkel & Blewett (1943*a*,*b*) have studied the dietetics of *O. surinamensis* and have shown that the larvae grow well on diets containing hygroscopic sugars such as fructose and sorbitol, and that this species seems to be better fitted than other dried-food insects to live on a diet with a high moisture content. It is also less dependent than, say, *Tribolium confusum* Duv. on the external supply of some B-vitamins because of the presence of intracellular symbionts in mycetomes embedded in the fat-body. The use as a food of the molasses in unrefined sugars might be expected in species that were even better adapted than *O. surinamensis* to a high sugar, high moisture diet. Fraenkel & Blewett (1943*b*) point out, however, that the best criterion for assessing the suitability of a diet for any insect is the length of larval life, *i.e.*, the time from hatching to pupation. This is undoubtedly long when *N. clavicornis* breeds in raw or yellow-crystal sugar, and this fact combined with the low egg-production of the females and the low viability of the eggs suggests that it is unlikely that the beetle could ever become a pest in such sugars. Wolcott's statement (1927, p. 221) that it is occasionally a pest of "brown" sugar in Haiti is not supported by L. Bonnefil (private communication, 1957) who can find no records of any serious infestations. The circumstances of the infestation of the experimentally stored raw sugar in Trinidad were quite exceptional as it is the practice of the sugar industry to avoid storing raw sugar for any length of time, especially during the wet season, because of the deterioration that takes place. No unrefined sugar can, however, be considered as a stable product in store, for although the proportion of molasses may be low, any circumstances leading to the uptake of water in the film may result in the establishment of moulds, bacteria and yeasts, all of which may bring about changes in its composition and render it more suitable for insect growth. Because adults of *N. clavicornis* are long-lived and because infestations are apparently limited to the periphery of even a small bulk of sugar, a slight increase in the multiplicative rate of this beetle would result in its being much more conspicuous. Since washed grey and yellow-crystal sugars are for direct consumption, any infestation is undesirable, but in terms of loss of sucrose the damage directly attributable to the beetle is likely to be small in comparison with that due to factors which operate increasingly with the uptake of moisture in any unrefined sugar.

Summary.

Nausibius clavicornis (Kug.) is a cosmopolitan Cucujid that has frequently been recorded from sugar. It is commonly found in this commodity in Trinidad, where it has not been collected from any other.

The adult and other stages are described, and an account is given of the life-history on Haydak's formula at 85°F. and 75 per cent. R.H. Development has also been studied on two types of unrefined sugar.

Copulation can take place within one day of the emergence of either sex and the female may begin laying within four days of copulation. The average number of eggs laid was 275 and the overall viability was 85 per cent. The average incubation period was just under five days.

The larvae of both sexes may undergo only five moults in development, but the more usual number for females is six. When larvae are disturbed during development, both sexes tend to have six larval instars. Severe disturbance may induce a seventh moult. The mean development period from oviposition to the emergence of the adult was 30 days when there were five larval instars; when there were six, development took about two days longer. Larval mortality on Haydak's formula was low.

Ovipositing females lived for up to 163 days under controlled conditions, but males tended to outlive females by about 50 days.

On unrefined sugars (*e.g.*, raw or yellow-crystal sugar), adults lived for almost as long (73 : 99) as on Haydak's formula, but oviposition was greatly reduced and the viability of the eggs was much lower. Larval mortality was high, especially in the first instar, and the total development period was greatly increased.

It is unlikely that *N. clavicornis* could multiply rapidly in raw or unrefined sugar, and any deterioration in stored sugar directly attributable to it would probably be small in comparison with that caused by other factors.

Acknowledgements.

Our thanks are due to Mr. M. E. G. Easton of Caroni Ltd. for bringing to our notice the infestation of the raw sugar storage experiment, and to the managers of all other sugar factories in Trinidad for allowing us to look for *Nausibius clavicornis* in their stores.

We are also grateful to the Commonwealth Institute of Entomology and the U.S. National Museum for supplying transcripts of early references: to the Sugar Research Department of the Imperial College of Tropical Agriculture for sugar analyses and information on sugar deterioration, and to Professor T. W. Kirkpatrick, in whose department most of this work was done, for much helpful advice and criticism.

References.

Anon. (1933). Exhibition of, and notes on local material, April 7, 1932.—*Proc. Hawaii. ent. Soc.* **8** pp. 217–219.

Back, E. A. & Cotton, R. T. (1926). Biology of the saw-toothed grain beetle, *Oryzaephilus surinamensis* (Linné).—*J. agric. Res.* **33** pp. 435–452.

Blackwelder, R. E. (1944–57). Checklist of the Coleopterous insects of Mexico, Central America, the West Indies, and South America. Parts 1–6.—*Bull. U.S. nat. Mus.* no. 185, 1492 pp.

Böving, A. G. (1921). The larvae and pupae of the social beetles *Coccidotrophus socialis* (Schwarz and Barber) and *Eunausibius wheeleri* (Schwarz and Barber) with remarks on the taxonomy of the family Cucujidae.—*Zoologica, N.Y.* **3** pp. 195–221.

Carr, D. S. & Harris, B. L. (1949). Solutions for maintaining constant relative humidity.—*Industr. Engng Chem.* **41** pp. 2014–2015.

Fraenkel, G. & Blewett, M. (1943*a*). Vitamins of the B-group required by insects.—*Nature, Lond.* **151** pp. 703–704.

Fraenkel, G. & Blewett, M. (1943*b*). The natural foods and the food requirements of several species of stored products insects.—*Trans. R. ent. Soc. Lond.* **93** pp. 457–490.

Haydak, M. H. (1936). A food for rearing laboratory insects.—*J. econ. Ent.* **29** p. 1026.

Howe, R. W. (1953). The rapid determination of the intrinsic rate of increase of an insect population.—*Ann. appl. Biol.* **40** pp. 134–151.

Howe, R. W. (1956). The biology of the two common storage species of *Oryzaephilus* (Coleoptera, Cucujidae).—*Ann. appl. Biol.* **44** pp. 341–355.

Kugelann, J. G. (1794). Verzeichniss der in einigen Gegenden Preussens bis jetzt entdeckten Käferarten nebst kurzen Nachrichten von denselben.—*Neu. Mag. Ent.* **1** pp. 513–582.

Lepesme, P. (1945). Les coléoptères des denrées alimentaires et des produits industriels entreposés.—*Encycl. Ent.* (A) **22,** 335 pp. Paris, Lechevalier.

Marsham, T. (1802). Entomologia Britannica, sistens insecta Britanniae indigena, secundum methodum Linnaeanum disposita. Vol. I.—548 pp. London.

Patton, W. S. (1931). Insects, ticks, mites and venomous animals of medical and veterinary importance. Part II. Public health.—740 pp. [Liverpool Sch. trop. Med.]

Redtenbacher, L. (1858). Fauna Austriaca. Die Käfer. Nach der analytischen Methode bearbeitet.—2nd edn., 1017 pp. Vienna.

Thomas, E. L. & Shepard, H. H. (1940). The influence of temperature, moisture, and food upon the development and survival of the saw-toothed grain beetle.—*J. agric. Res.* **60** pp. 605–615.

Wheeler, W. M. (1921). Notes on the habits of European and North American Cucujidae (sens. auct.).—*Zoologica, N.Y.* **3** pp. 171–183.

Wilson, J. W. (1930). The genitalia and wing venation of the Cucujidae and related families.—*Ann. ent. Soc. Amer.* **23** pp. 305–358.

Wolcott, G. N. (1927). Entomologie d'Haiti.—440 pp. Port-au-Prince, Serv. tech. Dep. Agric.

© Commonwealth Agricultural Bureaux, 1959.

A COMPARATIVE STUDY OF THE SOIL CONDITIONS FAVOURED BY CERTAIN MELOLONTHID AND TENEBRIONID PESTS OF TOBACCO IN SOUTHERN RHODESIA.

By G. H. Bünzli* and W. W. Büttiker.*

Melolonthid and Tenebrionid larvae often reach the level of major pests in the tobacco fields of Southern Rhodesia. Although the two types of insect frequently occur together in the same area, in any one severely infested site one type will be found to the exclusion of the other. No relationship between optimum sites and such ecological factors as climate and topography was detected for either type.

Melolonthid larvae, or white grubs, of the species *Anomala exitialis* Pér. and *Schizonycha profuga* Pér. on the one hand, and Tenebrionid larvae, or false wireworms, of the species *Psammodes similis* Pér. and *P. scrobicollis* (Fhs.) on the other, have their habitats in the light-textured granitic soils of the sand veldt. These soils are acid and exhibit no visible differentiation in their profiles; they carry a loose grass cover with irregularly scattered trees and shrubs, mostly of deciduous types.

Extensive soil surveys were carried out between 1949 and 1951 to select sites that would be suitable for some experiments on chemical control. It was noticed that false wireworms preferred soil with a substratum, especially when wet, of a lighter greyish-brown colour than that favoured by white grubs. Partial analyses were therefore made of a selected number of samples taken to a depth of 25 cm., in which zone the larvae mainly feed.

The results of mechanical analyses of five white-grub (A) and three false-wireworm habitats (B) are summarised in Table I, and for humus content an additional seven (A) and five habitats (B) were analysed (Table II).

TABLE I.

	A Habitat occupied by white grubs	B Habitat occupied by false wireworms
Skeleton	12·25 (4·2 – 26·7)	9·30 (8·4 – 10·7)
Fine earth (100%)		
Sands	82·50 (80·2 – 83·7)	86·33 (83·7 – 88·2)
Silt	11·02 (9·6 – 13·0)	8·97 (7·9 – 10·5)
Clay	6·48 (6·2 – 6·8)	4·70 (3·9 – 5·8)

The above analyses show that the soils of habitat B were lighter than those of A. Also the quantity of quartz particles of 2–5 mm. diameter, resistant to hydrolysis, was more variable in A than in B.

The clay and silt fractions in the top soils show local variations probably on account of slow sheet erosion of the very deep soils covering the semi-arid plateau that occupies so much of Southern Rhodesia. These local variations also have their influence, as one might expect, on the nature of the vegetation.

* Formerly of the Research Staff of the Tobacco Pest Control Research Scheme, Salisbury, Southern Rhodesia.

The organic matter in the soil in the two types of habitat were assessed and the results are given in Table II.

TABLE II.

	A Habitat occupied by white grubs	B Habitat occupied by false wireworms
Hygroscopic moisture	1·08 (0·53 – 2·60)	0·54 (0·40 – 0·67)
Loss on ignition	3·65 (2·37 – 5·07)	2·08 (1·40 – 2·77)
Total nitrogen	0·082 (0·067 – 0·103)	0·043 (0·030 – 0·053)

The above figures show a very marked difference between the two habitats. Carbon estimations were not made, but as these soils are free from carbonate, with little chemically combined water, the loss on ignition has been taken as a reasonably reliable indication of the humus content. The values for percentage loss on ignition have been plotted against the total percentage nitrogen (fig. 1) and this brings out clearly the differences between the types of soil in the two habitats.

If the conventional factor of 20 is accepted for the conversion of the nitrogen content to that of organic matter, soil A, which is favoured by white grubs, is

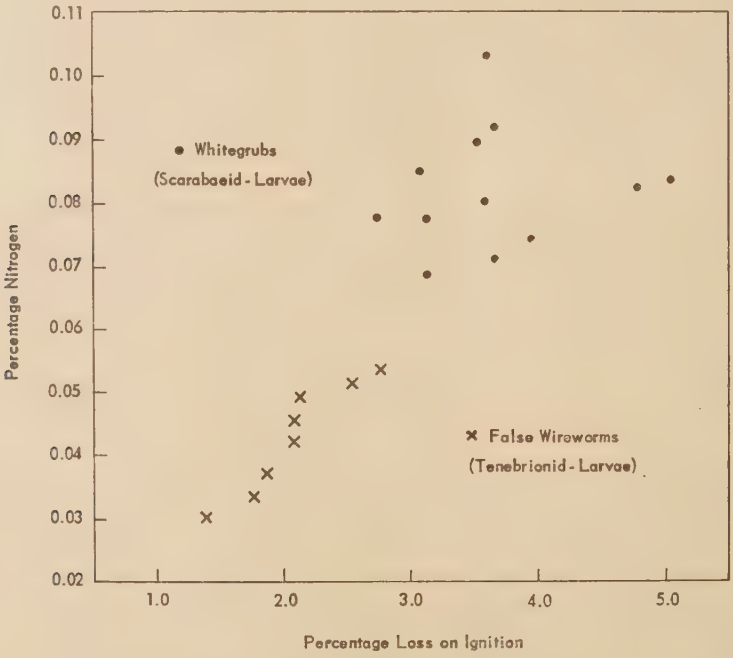


Fig. 1.—Relation between percentage nitrogen and percentage loss on ignition in samples from 12 white-grub and eight false-wireworm habitats.

seen to have on an average 1·64 per cent. organic matter whereas soil B, that favoured by false wireworms, has a corresponding figure of 0·86 per cent. Sandy soils with less than 1 per cent. organic matter are classified as "poor" in humus and those with between 1 and 2 per cent. as "fair". The habitats favoured by white grubs, therefore, are those with a definitely higher organic-matter content than the poorer soils occupied by false wireworms.

The two habitats differ essentially in the ratios of clay and nitrogen, the clay ratio of A to B being 1 to 0·725 and that of nitrogen 1 to 0·524. The soil of type A exhibits better colloidal properties, water retention capacity is enhanced, and moisture and temperature conditions in the substrata are better. These conditions favour the soft-bodied white grubs that require a soil which will facilitate their movements and not subject them to undue friction. In fact soil A has not only the physical properties but also the level of organic matter necessary to promote the successful development of Melolonthid larvae. The Tenebrionid larvae, on the other hand, can find their food requirements in soils of poorer nutritive value and with physical properties that would be unfavourable for white grubs.

The distribution ranges of the two types of insect overlap but there are no substantial incursions of Tenebrionids into the soils of higher fertility and clay content favoured by Melolonthids. The potential distribution of the latter is very wide. Collective swarming and migration over considerable distances has been observed and the adults consume more protein-rich green vegetation than those of the Tenebrionids. The fact that loamy sands, either occurring as islands or extensive areas adjacent to poor sands, are chosen year after year for oviposition suggests that the gravid females have olfactory sensoria that are well developed for detecting areas suitable for mass oviposition. The adult Tenebrionids, being incapable of flight, only move slowly over the surface of the soil and instances of sudden distribution over unusual distances have only been observed to take place as a result of flooding.

False wireworms, even in habitats that provide optimum conditions for them, are never found in large numbers because of the hostile attitude to each other adopted by these larvae. This may explain why the distribution range of the two Tenebrionid species here dealt with extends into areas of an almost semi-desert nature, with very sandy substrata and sparse plant growth.

Either type of larva may assume the nature of a pest in tobacco fields by supplementing its normal diet of dead organic matter in the soil with living tissues of the tobacco plants. Comparing areas carrying dense white-grub populations with those in which false wireworms were relatively abundant, it was found that heavy infestations of tobacco lands carried a population of 60,000 white grubs or more per acre whereas those of false wireworms rarely exceed 1,500.

The time required by the two species of Melolonthid (see page 259) to secure the full complement of food necessary for their development covers the 4 to 5 months of the wet season. The active feeding stages of the Tenebrionid larvae, on the other hand, are spread out over a period of 18 to 21 months, thus occupying both wet and dry seasons. Consequently, the Melolonthids have a one-year and the Tenebrionids a two-year life-cycle. There are, however, smaller Tenebrionids, such as species of *Gonocephalum*, *Zophosis* and other genera, that feed regularly on dead or living organic matter or both and have only a one-year cycle.

Mating in the case of the Melolonthids is facilitated by the habit of the beetles to congregate on plants when feeding. Tenebrionid adults (like their larvae), however, adopt a solitary existence and the mating call of the male is relied upon to bring together individuals of the opposite sex.

Two instances of attack by natural enemies on Melolonthid larvae are of interest as they both occurred in places where the humus content of the soil was

abnormally high. The analyses of the soils of these two habitats were not included in Tables I and II for that reason and because they only represented small island-like patches inside average white-grub infested tobacco fields. In one of these areas in the Norton District the top soil contained the abnormal amount of 0·18 per cent. nitrogen which imparted to the substratum a much darker brown colour than usual and parasitisation of the white-grub population by a species of *Tiphia* was found to occur. The open structure of the soil no doubt facilitated the entry of the beetles to oviposit but doubtless it also permitted access by the parasites later. The number of white grubs parasitised was found to be 3 per sq. yd. (25 per cent.), a higher degree of parasitisation than had been met with anywhere else. The second and larger area was in the Melfort District and was again characterised by having soil of a darker hue than the surrounding area. Here the nitrogen value varied between 0·13 and 0·15 per cent. This locality was revisited in two later consecutive seasons and found to harbour entomogenous fungi to which the white grubs succumbed. Detailed observations on this area have been the subject of a separate paper (Bünzli & Büttiker, 1959).

Neither insect parasites nor cryptogamic pathogens have been observed to affect the much less dense populations of false wireworms under field conditions.

Summary.

An investigation was made to determine the factors governing the distribution pattern of the larvae of certain species of Melolonthids and Tenebrionids; these are known to be serious pests of tobacco plants in Southern Rhodesia.

Observations were made on mixed populations of the white grubs, larvae of *Anomala critialis* Pér. and *Schizonycha profuga* Pér. (Melolonthinae), on the one hand, and on those of the false wireworms, larvae of *Psammodes similis* Pér. and *P. scrobicollis* (Fhs.) (Tenebrionidae), on the other.

It was found that the habitats favoured by white grubs had a higher clay, silt and organic matter content than those favoured by false wireworms. This was indicated by the darker brown colour of the soil; the clay ratio of the soils of the two types of habitat was as 1 to 0·725 and the nitrogen ratio as 1 to 0·524, respectively.

Heavy infestations of tobacco fields are associated with 60,000 white grubs or 1,500 false wireworms per acre. The white grubs complete their life-cycle in one year, the larvae obtaining the food requirements necessary for their development in the 4 to 5 months of the wet season. The false wireworms have a two-year life-cycle, the active feeding stages of the larvae being spread over 18 to 21 months, comprising both wet and dry seasons.

The infestations by the two classes of insect do not overlap in space to any great extent but are governed by the nature of the soil, the white grubs favouring areas in which the soil has a higher nutrient value and the false wireworms areas where the soil is poorer.

Reference is made to parasitisation of white-grub larvae in two areas, where the soil had an abnormally high nitrogen content, by a species of *Tiphia* in the one area and by entomogenous fungi in the other.

False wireworms have not been found to be similarly attacked under field conditions.

Acknowledgements.

The authors wish to thank the members of the Southern Rhodesian Tobacco Board and the Agro-Chemical Department of the Southern Rhodesian Government for the facilities and help extended to the Tobacco Pest-Control Research Scheme (1948–1952). They also take this opportunity to thank Dr. W. J. Hall,

formerly Director of the Commonwealth Institute of Entomology, London, for much constructive and helpful criticism of the draft of this paper.

Reference.

Bünzli, G. H. & Büttiker, W. W. (1959). Fungous diseases of lamellicorn larvae in Southern Rhodesia.—*Bull. ent. Res.* **50** pp. 89–96.

© Commonwealth Agricultural Bureaux, 1959.

BIONOMICS OF THE TEA RED SPIDER, *OLIGONYCHUS COFFEAE* (NIETNER).

By G. M. Das, M.Sc., D.I.C., Ph.D.(Lond.)

Senior Entomologist, Tocklai Experimental Station, Cinnamara, Assam.

From the very early days of tea cultivation, the red spider, *Oligonychus coffeae* (Nietn.), has been known as a pest of tea, *Camellia sinensis*, in north-eastern India, having been discovered in Assam in 1868. Subsequently it was noticed in Cachar and Darjeeling and other tea districts. It is now a widely distributed pest of tea in N.E. India, occurring in all tea estates in a more or less severe form, and it may be considered as the most serious of all tea pests if the total loss of tea caused by individual pests in this part of India is taken into consideration.

Watt & Mann (1903) give a comprehensive account of the early history of the pest in N.E. India. Wood-Mason (1884) in his brochure on tea pests describes it as a new species, *Tetranychus bioculatus*. Green (1890), however, identified it as the same species that occurs on coffee trees, described under the name *Acarus coffeae* by Nietner in 1861, but the workers on tea red spider in north-eastern India always called it *Tetranychus bioculatus* until Baker & Pritchard (1953) referred it to the genus *Paratetranychus*. Pritchard & Baker (1955) in their revision of the family Tetranychidae have, however, recognised *bioculatus* as a synonym of *coffeae* and assigned it to the genus *Oligonychus*.

Distribution and alternative Food-plants.

It was first recorded on coffee (Nietner, 1861) and later on tea in Ceylon (Green, 1890). It is a widely distributed pest of tea in north-eastern India and occurs in all tea districts under diverse climatic conditions. It occurs also as a minor pest of tea in southern India (Rau, 1941). It attacks jute, *Corchorus capsularis* (Misra, 1913, Das, 1948); Misra (1913) also recorded it on cotton, castor, mulberry, orange, indigo, *Triumfetta neglecta*, *Urena lobata*, *Hibiscus ficulneus*, *H. panduriformis* and *H. abelmoschus* as alternative hosts in India. Andrews (1928) found it on *Tephrosia candida* and *Derris robusta*, as well as on many jungle plants in tea-growing areas of N.E. India. The author recorded it on *Eugenia* sp., *Litsea lancifolia* and *Melastoma malabrathricum*. On tea in Ceylon it normally occurs in small numbers (Hutson, 1921) and has been observed on camphor, *Grevillea*, *Aristolochia* and *Eugenia cumini* (*jambolana*) (Light, 1927). It also occurs on tea in other countries, *viz.*, in Indonesia (Bernard, 1909), in Batum, U.S.S.R. (Demokidov, 1916), in Transcaucasia (Prostosserdov, 1917), in Formosa (Shiraki, 1920), in South Africa (Tucker, 1926), in Nyasaland (Smee, 1927) and in Indo-China (du Pasquier, 1932–33). In West-Indonesia, in addition to tea, it attacks a variety of plants including rubber, coffee, dadap, lamtoro, *Ixora* spp., etc. (*cf.* Light, 1927).

This species has also been recorded from Transvaal, South Africa, on *Parthenocissus quinquefolia*, from Brisbane, Australia, on *Quisqualis indica*, from Gainesville, Florida, on *Camellia*, and from Richmond, Florida, on *Melaleuca* sp. (Pritchard & Baker, 1955). In South Africa, a red spider found on tea and described as a new species under the name *Oligonychus merwei* by Tucker (1926) has been found to be identical with *O. coffeae* by Pritchard & Baker (1955).

Nature and Effect of Injury.

The damage to the tea plant is caused by the larval, nymphal and adult mites, which feed on the sap of the leaves and occasionally on the petioles. The adult males are almost always found wandering about in search of quiescent female deutonymphs and feed very little. The life of the male is short and this being so, the male causes very little damage.

A yellowish spot is first formed on the surface at the point of feeding, which subsequently turns brown. Repeated feeding in the vicinity increases the number of spots, which coalesce and form bigger spots or patches, and in course of time and with the activities of the increasing population, the injury extends to the whole of the surface. The damaged leaves later show a coppery brown discoloration, ultimately turning bronze, and may dry up and eventually fall off.

The attack is normally confined to the upper surface of older leaves, initially in shallow depressions of the surface, along the mid-rib and veins and, with the margin of the leaves curved over, as it is intensified, the mites spread to the whole of the upper surface, often going to the lower surface. In a severe infestation, particularly under conditions of drought, both surfaces are found to be more or less equally infested, the attack then extending to younger leaves.

Harrison (1938) suggested that old leaves, in which the cells are not turgid and the flow of the sap is slow, are preferred by red spider, while young leaves in a turgid condition with sap flowing freely are less attacked. He pointed out, however, that the young growth may lose its turgidity under conditions of drought, becoming liable to attack, and concluded that conditions tending to reduce the activity of growth of tea bushes are conducive to red spider attack.

In cases of severe injury, the growth of the bushes is very much retarded, and they may cease flushing more or less completely. Damage is particularly serious on bushes having poor reserves of starch in the roots after pruning. This is more evident where a severe attack is followed by a drought, when weak bushes and young plants may be killed outright.

The probable loss caused to tea as a result of red spider attack has been assessed in only one trial, carried out in 1932 and 1933 (Harrison, 1938). In 1932, which was a bad year for red spider, the control of the pest prevented a probable loss of 43 per cent. of the crop, but there was only 17 per cent. loss as a result of its attack in the following year, when the red spider was less serious. The cumulative effect on the health of the bushes as a result of repeated depredations by the pest is very serious; they gradually become weaker after each attack, and may later become economically unproductive unless they are brought back to normal conditions by judicious treatments.

Life-history and Habits.

Very little is known of the life-history of *O. coffeae* in north-eastern India. Earlier workers on tea pests in this region concentrated more on control than on a study of its life-history. In order to devise suitable control measures, particularly in respect of time and number of applications of acaricides, observations on the biology of the pest have been made at Tocklai during the past ten years and the results are briefly recorded here.

Copulation.

Both males and females are sexually mature on emergence. The males, however, emerge earlier and wander about in search of deutonymph females in the later stages. Pairings take place immediately on the emergence of the female. In most cases several males have been observed to surround a quiescent deutonymph female which on emergence admits one or more males. Andrews (1928) observed a female having admitted 14 males in succession. A female also admits

males several times during her oviposition period. Similarly a single male can fertilise several females.

Pre-oviposition period.

The female usually starts laying eggs within 24 hours of emergence (from March to June), but the pre-oviposition period may be prolonged in the cold weather and may last for 2 or 3 days. The unfertilised female usually lays its first egg a little later than the fertilised female.

Oviposition.

The eggs are laid singly at intervals on the surface of the leaves. A female usually lays 4–6 eggs per day, the highest recorded number being 10 eggs in one day. The maximum number of eggs laid by a female during her lifetime was 137, the average for 14 females being 91 eggs during the month of May (Table I). In the laboratory, fertilised and unfertilised females laid on an average almost the same number of eggs during their lifetime.

TABLE I.

Oviposition record from January to August at Tocklai (indoors).

Month (1958)	No. of females	Oviposition period (days)		Total no. of eggs laid		Highest no. of eggs laid by a female in one day
		Maximum	Average	Maximum by a female	Average per female	
Jan.–Feb.	11	23	18·2	65	44·9	6
Feb.	12	21	18·5	67	48·3	6
March	5	18	15·4	72	57·2	10
April	7	27	18·6	107	80·0	7
May	14	26	20·9	137	91·0	8
June	10	18	13·0	59	45·9	7
July	14	13	9·6	50	33·8	6
Aug.	10	16	10·2	52	36·1	7

Egg.

The egg is spherical, flattened on the lower surface where it is attached to the leaf surface and is, on an average, 0·11 mm. in diameter. A filamentous process arises from the upper pole and then bends in the form of a hook. The colour of the egg is blood red to chrome red, but before hatching it changes to light orange. Prior to hatching, the chorion splits along the side of attachment to the leaf surface and the young larva comes out through the slit. The egg-shell remains more or less intact unless mutilated by the mites or otherwise damaged.

The incubation period is 4 or 5 days during the months of May to September, but it may be as long as 13 days during the cold weather (Table II).

Larva.

The larva is six-legged, and is almost round. The freshly hatched larva is yellowish orange but the colour subsequently changes to pale orange, the abdomen later showing a somewhat greenish appearance with the consumption of food. The average length of the larva is 0·16 mm. and the average breadth is 0·12 mm. The larval period is followed by the first quiescent stage.

Protonymph.

The protonymph carries four pairs of legs instead of the three pairs present in the larva. The form of the body is somewhat oval. The legs and the anterior

part of the body are pale crimson, and the abdomen is deep reddish brown. The average length of 12 protonymphs was 0·20 mm. and the average breadth 0·13 mm. The active phase of the protonymph is followed by the second quiescent stage.

TABLE II.

Incubation period at Tocklai (outdoors).

Month (1948)	Incubation period* (days)	Av. mean temp. (°C.) during the period	Av. R.H. (%) at	
			8 a.m.	2 p.m.
Jan. ..	13	16·3	100·0	70·2
Feb. ..	11	16·1	100·0	60·8
March ..	8	20·8	98·7	62·1
April ..	6	23·8	95·9	60·5
May ..	5	25·6	89·5	70·8
June ..	4	26·4	94·0	80·0
July ..	4·5	27·9	93·5	83·0
Aug. ..	5	28·4	92·0	73·3
Sept. ..	5	27·3	94·2	74·8
Oct. ..	6	25·3	93·4	74·7
Nov. ..	8	23·1	96·2	65·9
Dec. ..	12	15·9	95·5	59·8

* This figure represents the period taken in the majority of the eggs hatched in each month.

Deutonymph.

There is very little difference between a protonymph and a deutonymph except in size. The sexes can be differentiated at this stage; the female is slightly bigger and has the abdomen rounded at the posterior end while the abdomen of the male is narrow. The average length of 12 deutonymph males was 0·23 mm. and the average breadth 0·14 mm., while the average length of 12 deutonymph females was 0·26 mm., the average breadth being 0·15 mm. After the third quiescent stage the adult emerges.

Duration of immature stages.

The time required for development from larva to an adult female is given in Table III. In the case of a male it is shorter by two to six hours during the summer months and may be by half a day in the cold weather.

Adults.

The male differs from the female in size and also in the form of the body. The female is nearly elliptical, the abdomen being broadly rounded at its posterior end. The legs and front portion of the body (propodosoma) are bright crimson in colour, while the abdomen is dark purplish brown. It is 0·32–0·44 mm. in length and 0·15–0·23 mm. in width. The male is smaller, and has a slimmer body, the abdomen being much narrower at the rear, and almost tapering to a point. The legs, particularly the first pair, are longer than those of the female. It has the same body colour as the female except that the tip of its abdomen is crimson. It is 0·27–0·31 mm. in length and 0·14–0·16 mm. in width.

Life-cycle.

There are several generations in a year but these overlap, and red spider mites in all stages of development can be found at almost any time throughout the year.

TABLE III.

Duration of immature stages from larva to adult female at Tocklai (outdoors).

Date of hatching (1948)	Date of emergence of adult (1948)	Approx. duration of larval stage (days)	Total duration of larval and nymphal stages	Climatic conditions from date of hatching to emergence of adult		
				Av. mean temp. (°C.)	Av. R.H. (%) at	
					8 a.m.	2 p.m.
4 Feb.	14 Feb.	2·5	10	15·9	100·0	63·0
5 „	16 „	2·5	11	15·7	100·0	62·7
16 „	27 „	2·5	11	17·5	99·5	56·8
19 „	1 March	—	11	18·7	97·4	56·4
29 „ *	8 „	2·0	8	20·7	96·6	47·5
13 March	21 „	2·0	8	19·1	90·1	60·6
14 „	22 „	2·0	8	18·7	89·8	60·6
28 „	6 April	2·0	9	22·3	89·2	59·0
13 April	21 „	2·0	8	23·0	94·0	72·8
14 „	21 „	1·5	7	23·1	93·3	72·8
15 „	22 „	1·5	7	23·3	92·0	68·5
9 May	16 May	1·5	7	26·0	90·6	77·4
10 „	17 „	1·5	7	26·6	87·8	74·3
11 „	18 „	1·5	7	27·1	85·6	69·7
22 „	30 „	—	—	—	—	—
7 June	13 June	1·0	6	28·9	87·9	77·5
22 „	29 „	1·5	7	29·2	91·8	70·0
11 July	19 July	2·0	8	27·8	92·4	70·7
13 „	21 „	2·0	8	28·2	90·1	68·1
14 Aug.	22 Aug.	2·0	8	28·8	91·9	75·8
7 Sept.	16 Sept.	2·0	9	27·4	94·8	77·3
8 „	17 „	2·0	9	27·5	94·0	76·4
21 Oct.	30 Oct.	2·0	9	22·7	92·2	63·4
10 Nov.	20 Nov.	2·5	10	21·3	93·1	65·8
11 „	22 „	3·0	11	21·1	92·9	65·5

* Leap year.

The duration of the life-cycle (from egg to adult) is shorter in the summer months and may be completed in 9·4–12 days in May and June, while it may take as much as 28 days in the cold weather (Table IV). The male emerges 2–6 hours earlier in the summer, but in the winter its life-cycle may be shorter by a day or two than that of the female.

TABLE IV.

Duration of life-cycle at Tocklai.

Dates of egg-laying	Average duration (days)	
	Indoors	Outdoors
17–22 Jan.	24·0	24·0
3–20 Feb.	20·1	19·8
4–20 March	15·4	16·6
6–20 April	11·1	12·8
4–19 May	10·3	12·0
4–18 June	9·4	11·0
6–8 July	11·0	12·3
10–12 Aug.	10·5	12·0
3–8 Sept.	12·0	13·0
15–16 Oct.	12·5	14·0
3–4 Nov.	18·0	19·5
7 Dec.	—	28·0 (one only)

Sex ratio.

It is always found that females constitute the great majority of the individuals found in the field. Since the adult males have a much shorter life it is to be expected that the number of males found on leaves in the field at any one time would be less than what it should have been from their actual number on emergence. Assessment of the emergence of adults was therefore made in the laboratory to determine the exact ratio between males and females (Table V).

TABLE V.

Numerical ratio of males to females (indoors).

Month (1958)	No. of males	No. of females	Ratio
March ..	141	399	1 : 2·83
April ..	137	184	1 : 1·34
May ..	184	297	1 : 1·56
June ..	326	356	1 : 1·09
July ..	147	153	1 : 1·04
Aug. ..	105	106	1 : 1·01

Though the males are found in smaller numbers in the field it is unlikely that many females lay eggs without being fertilised, as one male can fertilise several females and there are always sufficient males available for fertilisation of all the females on emergence. Parthenogenetic reproduction may, however, take place under induced conditions, the progeny being all males.

Length of life.

The female usually dies soon after the last egg has been laid, but occasionally she may live a day or two more. The maximum life of a female was found to be 29 days with an average of 24·4 days for seven females during the month of April. The males usually die within four or five days under field conditions. If, however, they remain unmated, they may live longer, and the maximum length of life of one of a batch of unmated males was found to be 12 days in the month of April, the rest having died earlier.

Habits.

The red spider mites live under the cover of a silken web which they spin over themselves as a protection against inclement weather. The shallow depressions that characterise the condition known as "matted leaf", are suitable for securing the threads and at the same time leave sufficient room underneath in which the mites can move about freely; these depressions are selected by the mites in the first instance as places in which to establish themselves, although they spread to the whole of the surface later on.

The red spider prefers bright sun, and consequently unshaded tea is more severely attacked than tea under shade trees (Andrews, 1920; Harrison, 1938). It may be mentioned here that on jute, *Corchorus capsularis*, it remains almost invariably on the lower surface of the leaf.

Seasonal History.

The red spider is active and breeds on tea throughout the year in N.E. India. On pruned tea, the attack is marked early in March, while on unpruned and "skiffed" * tea, it is evident even earlier. With the rise in temperature, the rate of multiplication is increased, and generations follow in quick succession, resulting in a heavy build-up of population in late March or in April. It continues to cause severe injury in May and June until the monsoon rains set in, when most of the active forms are washed off and fail to regain the bushes. From July it almost disappears from tea unless there is an abnormally dry period. At the termination of the rainy season, the infestation starts again, but it rarely becomes serious. During the cold weather, the rate of multiplication is considerably reduced, and the population that usually persists on bushes in December and January is extremely low, although young tea is sometimes found to be heavily infested.

It was held that the red spider mites hibernate in the cracks and crevices of the tea bush or in the soil during the cold weather (Carpenter & Antram, 1911; Hope, 1915). Andrews (1928) stated that when tea is heavily pruned, they may enter into a kind of hibernating stage in the crevices of the bark on the stems, or in the soil, but wherever there are leaves on tea bushes they may be on old leaves here and there at any time of the year. He also pointed out that the "fish-leaves" or "janums" † are favourable haunts. Comrie (1939), however, found red spider occurring on the tea bushes at Tocklai throughout the cold weather and assumed that anything that would reduce the amount of leaf during this period would have a beneficial effect in reducing the incidence of red spider.

Investigations pursued by the author during the last few years show that red spider does not pass the winter in hibernation. It continues to breed during the cold weather and can be found in all stages of development on a few old leaves, but only in small numbers on pruned bushes, and in slightly greater numbers on unpruned and skiffed bushes and young tea. These mites are primarily responsible for damage to tea when conditions are favourable for their multiplication. Any mites present on prunings usually perish and the few that may be able to crawl

* Just a little cut-off at the top of all shoots, some time after plucking is over.

† Imperfect unserrated leaves above the bract of a new shoot.

back on to the bushes, and subsequently establish themselves, play a negligible part in the injury. Bushes defoliated after pruning as a preventive measure, therefore, suffer little from red spider attack, whilst medium or heavily pruned tea, where only thick stems are left on bushes and the new growth comes away much later, is least affected.

Dispersal of red spider mites is effected by various means; obviously it may spread from infested areas to healthy areas but defoliated and medium pruned teas are hardly affected unless there is a heavy migration of mites from heavily infested adjacent areas.

Amongst the factors that influence the incidence of red spider and the intensity of its attack, weather conditions play an important part. Prolonged dry weather during the early part of the flushing season normally increases the red spider. Intermittent slight rains have little effect but red spider is unable to withstand continued heavy rains.

The susceptibility of kinds or "jats" of tea to red spider attack, and the influence of manuring, pruning and other agricultural practices on its incidence will be dealt with in a separate paper.

Dispersal.

The attack on a bush is spread chiefly by the adult females, but nymphs also disperse from heavily infested leaves. The bushes touch each other, and it is natural to expect that mites will migrate from bush to bush by crawling. On a badly infested bush, the top is found to be heavily webbed, threads extending from leaf to leaf and to adjacent bushes, and the mites are found crossing in large numbers to other bushes.

Dispersion is also effected by wind, which carries the mites for considerable distances. The mites are occasionally found suspended on long threads, and in this way they can be carried by wind. Labourers working in the tea are also responsible for spreading the attack by carrying the mites on their clothes and in their baskets. Cattle, goats, birds and insects too play an important part in dispersion, carrying the mites on their bodies and legs.

Predators.

The following predators were observed to attack red spider, often keeping it in considerable check.

1. *Verania vincta* Gorham (Coccinellidae)
2. *Stethorus* sp. (Coccinellidae)
3. *Jauravia* sp. ,,
4. *Scymnus* sp. ,,

The larvae and adults of the above Coccinellids feed on the eggs and other stages of the red spider.

5. *Chrysopa* spp. The larvae of two species of *Chrysopa* are occasionally found in the colonies of the red spider, feeding mostly on the active stages of the mite.
6. Staphylinid beetles. The larvae and adults are often found in the colonies, feeding mostly on the eggs.

Summary.

The red spider, *Oligonychus coffeae* (Nietn.), is the most widely distributed and probably also the most serious pest of tea in north-eastern India, and also occurs on tea in other parts of India and in other countries. It attacks jute, *Corchorus capsularis*, in India and has been recorded on a wide variety of other plants in India and other countries.

The life-history of *O. coffeae* in north-eastern India is described. The duration of the life-cycle varies with the season depending on the temperature and humidity.

In May and June the life-cycle is completed in 9·4–12 days outdoors, while in the cold weather it may take as much as 28 days. The maximum length of life of a female has been found to be 29 days indoors. The males usually die within four or five days. Parthenogenetic reproduction may take place under induced conditions, the progeny being all males.

Red spider normally attacks the upper surface of the mature leaves in which the sap is not flowing freely. In a severe infestation, particularly under conditions of dry weather, the lower surface and the young leaves are almost equally attacked. The affected leaves turn brown, then bronze, and may eventually dry up and fall off.

The red spider mites live under a cover of web that they spin as a protection against inclement weather. The pest occurs in severe form from March to June but with the monsoon rains it practically disappears. A second, light, attack may, however, develop in September or October.

During the cold weather, the mites are present in very small numbers on a few old leaves of the tea bushes, and with the rise in temperature in the spring, they multiply rapidly, resulting in subsequent heavy infestations.

Various factors influence the incidence of red spider and the intensity of its attack. Pruned bushes properly cleaned out are less affected. Bushes defoliated after pruning, and medium pruned tea remain practically unaffected. Prolonged dry weather during the early part of the flushing season normally increases the red spider incidence. It prefers bright sun and unshaded areas are more severely attacked.

The red spider spreads from bush to bush by crawling. Dispersal is also effected by various agencies such as wind, cattle, goats and labourers.

A number of predatory insects attack eggs and other stages of the red spider, often keeping it considerably in check.

Acknowledgements.

The author is grateful to the Director, Tocklai Experimental Station, for permission to publish this paper.

References.

Andrews, E. A. (1920). Insect pests of tea in north-east India during the season 1919.—*Quart. J. Indian Tea Ass.* **1920** pp. 27–36.

Andrews, E. A. (1928). Red spider.—*Quart. J. Indian Tea Ass.* **1928** pp. 206–219.

Baker, E. W. & Pritchard, A. E. (1953). A guide to the spider mites of cotton.—*Hilgardia* **22** pp. 203–234.

Bernard, C. (1909). Over de ziekten der theeplant veroorzaakt door mijten.—*Meded. Proefst. Thee* no. 3, 117 pp.

Carpenter, P. H. & Antram, C. B. (1911). Cold weather work.—*Quart. J. Indian Tea Ass.* **1911** pt. 4 pp. 1–13.

Comrie, L. C. (1939). Proceedings of the Third Annual Conference, Indian Tea Association pp. 13–14.

Das, G. M. (1948). Insects and mite pests of jute.—*Sci. & Cult.* **14** pp. 186–190.

*Demokidov, K. E. (1916). On the life-history of the tea moth, *Parametriotes theae*, Kusn.—*Rev. russe Ent.* **15** pp. 618–626. (*Rev. appl. Ent.* (A) **4** p. 334.)

* Original not seen.

Green, E. E. (1890). Insect pests of the tea plant.—104 pp. Colombo.

Harrison, C. J. [1938]. The occurrence and treatment of red spider on tea in north east India.—*Memor. Tocklai exp. Sta. Indian Tea Ass.* no. 2, 26 pp.

Hope, G. D. (1915). Addresses to Darjeeling planters.—*Quart. J. Indian Tea Ass.* **1915** pp. 100–108.

Hutson, J. C. (1921). Scale insects and mites upon tea.—*Trop. Agriculturist* **56** pp. 378–380.

Light, S. S. (1927). Mites as pests of the tea plant.—*Trop. Agriculturist* **68** pp. 229–238.

Misra, C. S. (1913). The red spider on jute (*Tetranychus bioculatus*, Wood-Mason).—*Agric. J. India* **8** pp. 309–316.

*Nietner, J. (1861). Observations on the enemies of the coffee tree in Ceylon.—31 pp.

du Pasquier, R. (1932–33). Principales maladies parasitaires du théier et du caféier en Extrême-Orient.—*Bull. écon. Indochine* **35** pp. 223B–253B, 367B–415B, 589B–618B, 689B–720B; **36** pp. 1–144.

Pritchard, A. E. & Baker, E. W. (1955). A revision of the spider mite family Tetranychidae.—*Mem. Pacif. Coast ent. Soc.* **2,** 472 pp.

*Prostosserdov, N. N. (1917). The cultivation and treatment of tea in Transcaucasia.—60 pp. Petrograd. (*R.A.E.* (A) **5** p. 454.)

Rau, S. A. (1941). Report of the Entomologist.—*Rep. Tea sci. Dep. U.P.A.S.I. 1940–41* pp. 41–50.

Shiraki, T. (1920). Insect pests of the tea-plant in Formosa.—*Proc. 3rd ent. Mtg Pusa* **2** pp. 629–669.

Smee, C. (1927). Report of the Entomologist.—*Rep. Dep. Agric. Nyasaland 1926* pp. 13–20.

Tucker, R. W. E. (1926). Some South African mites. Mainly Tetranychidae and Eriophyidae.—*Mem. Div. Ent. Dep. Agric. S. Afr.* no. 5 pp. 3–15.

Watt, Sir G. & Mann, H. H. (1903). The pests and blights of the tea plant.—2nd edn., 429 pp. Calcutta.

Wood-Mason, J. (1884). Report on the tea-mite and the tea-bug of Assam.—20 pp. London.

* Original not seen.

© Commonwealth Agricultural Bureaux, 1959.

TRANSECT FLY-ROUNDS IN FIELD STUDIES OF *GLOSSINA*.

By J. Ford,* J. P. Glasgow, D. L. Johns and J. R. Welch

East African Trypanosomiasis Research Organisation.

Introduction.

One of the earliest observations made in field research on tsetse flies (*Glossina*) was that their distribution is related in some detail to the distribution of vegetation communities. The relationship has been explored by numerous workers, the main technique used being the "fly-round" or, more precisely, the "extended reconnaissance fly-round" as defined by Potts (1930). The use of the word "round" derives from the earlier practice of visiting in turn a number of selected localities to make timed catches of tsetse flies. Separately recorded catches were also made of tsetse flies attacking the catching party during its passage from one locality to the next. Eventually the practice of making timed catches was dropped and data were only recorded as between, and not at, fixed points. The word "round", with its implication of a return to the starting point, was often a misnomer, since many fly-rounds did not do this.

The fly-round was a path, usually about five miles long, cut through the bush in such a way that it traversed the principal vegetation communities (defined on a floristic basis). It was divided into sections corresponding to these communities, and the catch recorded separately for each section. The numbers of tsetse caught on each section, or on different fly-rounds, were compared by using the convention of "apparent density" (A.D.) or the number of non-teneral † male tsetse per 10,000 yards. One could then say of a particular vegetation community that it had, within perhaps rather wide limits, a certain characteristic apparent density, with a certain percentage of female and of teneral flies, while other statistics could be collected as desired. The fly-round, so used, formed the technical basis for planning numerous reclamation schemes and was a technique of the highest value. But it had certain limitations. The division into sections corresponding to vegetation communities and the calculation of various statistics for each community resulted in the tacit assumption that the tsetse population was more or less evenly distributed throughout each community. Differences in value for the populations of two communities might be related to their floristic composition, game population, internal visibility (dependent on density of vegetation) and climate. However, these relationships tended to remain rather vague, since, in general, they were not made the subject of observations which could be quantitatively correlated with the fly-round data.

In about 1946 our colleague, Dr. P. E. Glover, introduced the use of belt transects (Tansley & Chipp, 1926) for the quantitative description of *Glossina* habitats. It was soon realised that a slight modification of this technique might provide a much improved method of working fly-rounds. At Shinyanga, Tanganyika, an area known as Block 9, comprising some 50 square miles of thornbush infested with *Glossina swynnertoni* Aust. and *G. pallidipes* Aust., had been earlier covered by a rectangular grid of paths dividing it into squares with sides

* Now of the Tsetse and Trypanosomiasis Control and Reclamation Department, Salisbury, Southern Rhodesia.

† Flies after their first blood-meal.

of 2,000 yards (Harrison, 1936). For some years, six sides of two diagonally adjoining squares (fig. 1) had been used as a normal fly-round (No. 5), being divided into nine sections according to the major vegetation communities through which they passed. Since, unlike other fly-rounds in use at Shinyanga, No. 5 followed an arbitrary course along straight lines, it could be used to compare the new with the old method. It was therefore redivided into 120 sections of 100 yd. each. The distribution of non-teneral males of *G. swynnertoni* over the fly-round

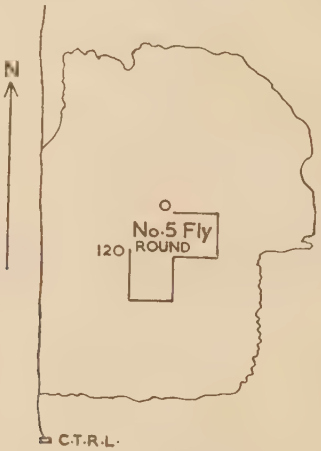


Fig. 1.—Block 9 at Shinyanga, Tanganyika, according to Harrison (1936), showing No. 5 fly-round.

using the old method of collecting data on nine sections based on vegetational differences is compared, in fig. 2, with the distribution obtained by the use of the new method. The much greater detail provided by the short sections is very clear.

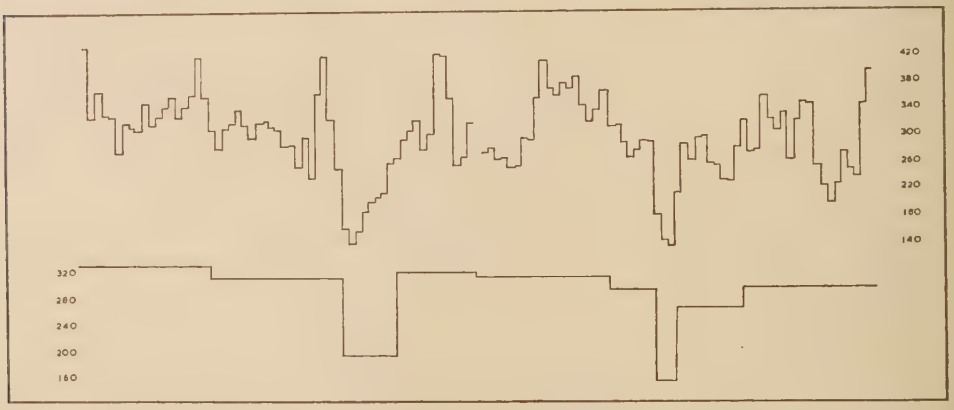


Fig. 2.—The distribution of non-teneral males of *G. swynnertoni* on fly-round No. 5 at Shinyanga, Tanganyika. Transect fly-round results (catch per 100-yd. section per month) are shown in the upper histogram, and those of the old-type fly-round (catch per 100 yd. of the long sections per month) in the lower. Data obtained between March 1949 and February 1951.

It was now apparent that the straight fly-round with numerous sections of short arbitrary length had many advantages and before long it was widely

adopted under the name of " line transect " or " transect fly-round ". Buxton (1955, Appendix 5) refers to this type of fly-round but states that it has not been fully or critically described. The present paper in part repairs that omission.

Because the transect fly-round was straight, it traversed all vegetation types in the proportion in which they occurred, subject, of course, to errors of random sampling. It avoided the pre-supposition, inherent in the earlier type of fly-round, of a certain type of vegetational relationship with fly density, while the shorter sections enabled density distribution to be described with much greater accuracy. Another advantage was that catches were standardised. Fly-boys now stopped to catch at the numbered section posts; formerly they were supposed to stop at regular intervals, but wide individual variations in practice accentuated unavoidable personal differences between the catches of individual fly-boys.

The old type of fly-round necessarily involved a good deal of preliminary exploration of the bush, in order that vegetation types might be defined and the fly-round directed through them. The transect round, provided its direction was orientated correctly in relation to topography, could be based on compass bearings to cut most of the vegetation types in an area since, in general, these tend to be arranged according to a catenary pattern of soils controlled by topography (Morison, Hoyle & Hope-Simpson, 1948). An African assistant, without any knowledge of vegetation communities, could therefore set out a fly-round and begin the collection of quantitative data on tsetse density which could subsequently be related to other measured features of the round.

In its simplest form, the transect fly-round is a straight path divided into equal sections usually 50 or 100 yd. long. The use of the word " round " here is only justified by the usage of many years; other patterns, however, may be used. It is the division of the line into arbitrary section lengths which is the essential feature. Jackson (1955) used the standard-length section as a means of describing the distribution of *G. morsitans* Westw. in relation to vegetation communities and game distribution. In his work and other, unpublished, work of our own, the fly-round, in order to yield intensive information about a small area, was disposed in an angular spiral instead of a straight line. Only in the case of *G. palpalis fuscipes* Newst. is a geometrical lay-out not used. This is because the habitat of this species follows the shores of rivers and lakes, although it is again an advantage to divide the catching path into short sections of arbitrary length.

Variation in Section Length.

The transect fly-round may be varied in respect of the length of its sections. This has been investigated with three species of tsetse, namely, *G. swynnertoni*, *G. pallidipes* and *G. austeni* Newst.

(*a*) *G. swynnertoni*.

Three transect rounds at Shinyanga (Nos. 6, 7 and 8), each 2,000 yards long, were set out parallel to one another and 400 yards apart. Each was divided into 40 sections of 50 yd. each, and all three rounds were caught-over simultaneously six times a week. Catches were made in opposite directions on alternate days and were arranged so that catching points on the three rounds on any day were 50, 100 or 200 yd. apart. In each week any one round was worked twice with catching points at each of three different distances. The complete series was repeated 12 times throughout a year. The results are shown in Table I.

It will be seen that progressively fewer flies of all categories, except teneral males, were caught as the interval between catching points was increased. The relative proportions of the various categories were not significantly changed.

TABLE I.

Total catches of *G. swynnertoni* on fly-rounds 6, 7 and 8 at Shinyanga, Tanganyika.

	Section length		
	50 yd.	100 yd.	200 yd.
Non-teneral males:			
Round no. 6	498	303	286
Round no. 7	450	444	285
Round no. 8	568	392	381
Total	1516	1139	952
Mean apparent density ..	315·83	237·29	198·33
Non-teneral females :			
Total	117	110	83
% of total adults ..	7·16	8·81	8·02
Teneral males :			
Total	65	58	63
% of total males ..	4·11	4·85	6·21
Teneral females :			
Total	62	49	44
% of total young flies	48·81	45·79	41·12

Data obtained at irregular intervals between April 1951 and March 1952. Difference between non-teneral catches at 50 and 100 yd. significant ($P < 0{\cdot}02$). Difference between non-teneral catch at 100 and 200 yd. significant ($P < 0{\cdot}05$).

TABLE II.

The results of catches of *G. pallidipes* on 25-yd. and 100-yd. sections on two fly-rounds at Ruma, Lambwe Valley, Kenya, 1953.

Path	Month	25-yd. sections				100-yd. sections			
		N.T.♂	N.T.♀	T.♂	T.♀	N.T.♂	N.T.♀	T.♂	T.♀
Red	Jan.	2165	5	6	4	1987	2	5	2
	Feb.	1286	4	3	4	1246	1	3	3
	Mar.	2054	4	7	9	1796	4	7	4
	Total	5505	13	16	17	5029	7	15	9
	A.D.	193·36				176·64			
Black	Jan.	2319	8	4	10	2231	5	3	3
	Feb.	1476	5	2	4	1533	5	4	2
	Mar.	2360	6	9	7	2234	6	11	4
	Total	6155	19	15	21	6018	16	18	9
	A.D.	153·30				149·89			

Tests of significance of difference between catches using 25-yd. and 100-yd. sections:

Non-teneral (N.T.) ♀♀ .. .. $P=0{\cdot}3$
Teneral (T.) ♂♂ .. .. .. $P=0{\cdot}9$
Teneral ♀♀ .. .. $P=0{\cdot}01$
All teneral flies .. .. $P=0{\cdot}1$

(*b*) *G. pallidipes*.

An experiment lasting three months was carried out in the Lambwe Valley, in the Nyanza Province of western Kenya. Two concentric and angularly spiral fly-rounds (Jackson, 1955), 75 yards apart, were used; they were termed the "red" and "black" paths. The "red" path was 3,900 and the "black" 5.500 yd. long. On any day, a catching party of four men caught on 25-yd. sections on one fly-round while a similar party simultaneously caught on 100-yd. sections on the other. The fly-rounds were traversed in opposite directions on alternate days and the two catching parties changed fly-rounds every two days. Results are given in Table II. For the greater part of their lengths, both rounds passed through dense continuous thicket, the main habitat of *G. pallidipes*, although some open country where few flies were caught was also sampled. The apparent density on the "red" round exceeded that on the "black" because less of the "red" extended into open country.

These results show that, in general, the shorter sections produced the larger catches, but only in the case of the small samples of teneral female flies was the difference significant.

(*c*) *G. austeni*.

Six pairs of catches on 50- and 100-yd. sections were made along an 800-yd. length of a fly-round in the Jozani Forest, Zanzibar. Only one catching party, with a bait ox, was available for this work. The fly-round was traversed in one direction, beginning at 8 a.m., using one section length, and in the opposite direction at 10.30 a.m., with the other section length. This arrangement was alternated daily. The results appear in Table III.

TABLE III.

Catches of *G. austeni* along 50- and 100-yd. sections on one fly-round in Jozani Forest, Zanzibar, 1950.

	50-yd. sections				100-yd. sections			
	N.T.♂	N.T.♀	T.♂	T.♀	N.T.♂	N.T.♀	T.♂	T.♀
Catch	175	24	20	8	153	14	15	9
A.D.	365				319			

Tests of significance of difference between catches using 50-yd. and 100-yd. sections:

Non-teneral (N.T.) ♂♂ .. .. $P=0{\cdot}7$
,, ♀♀ .. .. $P=0{\cdot}2$
Teneral (T.) ♂♂ .. .. .. $P=0{\cdot}5$
All teneral flies .. .. $P=0{\cdot}7$

As with *G. pallidipes*, although the catch of all categories of flies (excepting teneral females) tends to be larger on the shorter sections, differences are not significant.

Conclusion on section length.

In the case of *G. swynnertoni*, the increase of section length from 50 to 100 yd., or from 100 to 200 yd., resulted in a significant decrease in the catch.

With *G. pallidipes* and *G. austeni* similar tendencies were not statistically significant. It is evident, however, that with both the latter species there must be a point at which increasing disparity between section lengths would significantly affect the catch.

There is no suggestion in these results that the catch at each stop is related to the number of flies only in the near vicinity of the catching site. If this were so, the catch with sites 25 yd. apart might be expected to be four times, and those 50 yd. apart to be twice, the catch at sites 100 yd. apart. The evidence suggests that tsetse are attracted to the party all along the path and that differences between the catches can be accounted for by the failure of a proportion of the flies to follow the full length of the longer sections.

The loss with increasing distance is small with *G. pallidipes* and *G. austeni*, both of which inhabit thicket and have very low standard availabilities (apparent density divided by population per sq. mile). It is relatively high in *G. swynnertoni*, which inhabits open grassed woodland and has a higher standard availability. *G. swynnertoni* is thought to have a higher availability because it finds man a more attractive host, but this conception does not seem to fit the facts recorded here, which suggest that the species that finds man more attractive follows him least.

Fluctuation in the Catch.

Lloyd, Johnson & Rawson (1927) pointed out that the number of tsetse caught on any occasion was a function not only of the true density of the population, but also of its activity (often now called availability), or the readiness of individual tsetse to come to the catchers. They spoke of the catch as being a measure of "density activity". The activity or availability of the tsetse population is affected by a variety of factors which have been discussed by several authors whose views are summarised by Buxton (1955). It seems necessary again to refer to this problem, illustrated in Table IV, where a four-to-one difference between the highest and lowest catch of *G. pallidipes* is recorded on a fly-round done each weekday for a month. This fly-round was divided into 156 sections each 25 yd. long. The catches on the 7th and 8th days, for example, are statistically very significantly different. This was shown by subtracting for each section the catch on the 7th day from the catch on the 8th; the frequency distribution of the differences was as follows:

Difference	−3	−2	−1	0	1	2	3	4	5	
No. of sections	5	5	10	68	16	21	10	12	9	Total 156

The mean difference, + 0·9359, is more than six times its standard error.

TABLE IV.

Daily catches of non-teneral males of *G. pallidipes* at Ruma, Lambwe Valley, Kenya, in June 1953.

244	61	170	144	126
116	207	198	249	116
216	142	162	121	
140	114	228	176	
229	109	138	183	
128	193	178	113	

Mean catch = 161·58 Maximum catch = 249 / Minimum catch = 61 } Ratio 4·08 : 1

It is clear that each day's catch is the resultant of the density of the population and its availability to the catching party. The increase from 61 on the seventh to 207 on the eighth day must be due to increased availability, not to an augmented population. Availability, as used here, has a composite meaning which included the effect of climate, the physiological state of the tsetse (hunger, for example), visibility and the reaction of the flies to movement. Jackson (1937) showed that availability changed to some extent with season. The diurnal change was recognised, in extreme form, by Potts (1930) when he noted the very low availability of tsetse at night. In most field studies, steps are taken to minimise variability of this sort, by standardising the time of day at which fly-rounds are done, and in numerous ways the " density-activity " nature of the catch is recognised. There is a third element, however, less often taken into account. Lloyd, Johnson & Rawson (*loc. cit.*) also showed, at least by implication, that the behaviour of the catching party (apart from its competence at catching) was of importance, for they noted that *G. tachinoides* Westw. came in abundance to stationary catchers, but that in order to attract numbers of *G. morsitans*, movement was necessary. It is evident that under the heading " Variation in Section Length " (p. 277 above), we are dealing with a similar phenomenon, namely, the alteration in magnitude of the catch by a change in the behaviour of the catching party. In West African practice the reduction of the catch to a mean " fly-boy-hour " takes cognizance of one aspect of catching-party behaviour, namely its size.

It is clear that in using any of the conventional measures of " density activity ", such as " apparent density ", the behaviour of the catching party must be stated: its size, the frequency of catching, special baits used and time of day for operation. Too often the apparent density is given as a measure of tsetse density without any indication of how it is obtained.

The day-to-day variations as illustrated in Table IV, however, are due to factors influencing availability which cannot be controlled.

The Detection of Concentrations.*

The variations due to changes in availability are commonly noted between catches at different times. A consideration of the variations in composition of the catch at different points on the fly-round (such as hunger-stage proportions, female and teneral percentage) shows that availability must also change from place to place. It is one of the advantages of transect fly-rounds that data may be subjected to simple statistical treatment. Since such a round has numerous short sections of arbitrary length, it is quite simple to test whether the catches are randomly distributed or not. If they are not, the fly-round may have passed through a " concentration site ", or through an area avoided by the tsetse, or both. Strictly speaking, we must note that a " concentration site " is an area in which the catching party is attacked or approached by a relatively large number of tsetse flies; an area avoided is an area in which the number of tsetse seen is less than expected. It is an assumption that the real population is greater or smaller in the area concerned. The mean catch per section is first calculated, usually that of non-teneral males, although the method is equally applicable to other categories of flies if the data are sufficient. By calculating the Poisson series for this mean catch, we can determine the probability of making a catch of 0, 1, 2, 3 . . . tsetses in any one section. If the mean catch per section

* Our colleague, Mr. F. Isherwood, has recently pointed out that the logic of this section is not impeccable, in that the method proposed is not an efficient way of ascertaining whether or not catches are randomly distributed. The practice of grouping sections with zero catches, as in the top left-hand corner of Table V, is also not strictly valid. However, in practice, interest centres on departures from random such that some sections yield catches unexpectedly high, and the method proposed here provides a way of detecting such sections that is rapid and at least more objective than the completely arbitrary methods used in the past.

is, for example, 10, the probability of catching 0 in any one section is very small. The probabilities rise for each succeeding term of the series to a maximum of 10, after which they decline until the probability of catching 17 or more in any one section is again quite small. Taking the conventional 5 per cent. level of probability as showing significance, we can calculate high and low thresholds corresponding to any mean catch per section, such that if the tsetse are occurring at random throughout the bush, 95 per cent. of the catches will be within the thresholds and $2\frac{1}{2}$ per cent. above the high threshold and $2\frac{1}{2}$ per cent. below the low threshold. Catches lying outside the thresholds can be regarded as significantly high, or low. If, in a fly-round having a mean catch of 10 per section.

TABLE V.

Significantly high, and low, section catches for mean values of catch per section from 0·1 to 100.

Low threshold	Mean catch per section	High threshold
37 zeros	0·1	2
18 zeros	0·2	2
12 zeros	0·3	2
9 zeros	0·4	3
7 zeros	0·5	3
6 zeros	0·6	3
5 zeros	0·7	3
5 zeros	0·8	3
4 zeros	0·9	4
3 zeros	1·0	4
3 zeros	1·25	4
3 zeros	1·5	5
2 zeros	1·75	5
2 zeros	2·0	6
2 zeros	2·5	6
1 zero	3·0	7
1 zero	3·5	8
1 zero	4·0	9
1	5·0	10
1	6	12
2	7	13
3	8	15
3	9	16
4	10	17
4	11	19
5	12	20
6	13	21
7	14	22
7	15	23
8	16	25
9	17	26
10	18	27
11	19	29
11	20	30
15	25	36
19	30	41
23	35	47
27	40	53
32	45	60
36	50	65
45	60	75
54	70	87
62	80	98
72	90	110
80	100	125

there were 100 sections, and if the flies were randomly distributed, then $2\frac{1}{2}$ sections would have a catch of 17 or more. Any section with a catch above the threshold will be regarded with interest, however, and if the observation can be repeated, the existence of a concentration (or of an area of avoidance by tsetse) can be regarded as established, since high (or low) catches due to random causes would not tend to recur in the same place. Such information is likely to be particularly useful in connection with reclamation work.

High and low thresholds corresponding to mean catches per section of from 0·1 to 100 are given in Table V. The Table is entered by the middle column, and the high and low thresholds corresponding to the calculated mean catch per section are read off. If the mean catch per section is 10, the low threshold is 4, and the high threshold is 17. In tabulating results it is helpful to mark sections below the low threshold with a blue pencil and sections above the high threshold with a red. If the results for the next period (day, week, month) are entered on the next line, the movement of concentrations with time may be conveniently demonstrated. An actual example of this practice is shown in fig. 3.



Fig. 3.—The detection of concentrations on transect fly-rounds. Cross-hatching indicates sections with significantly high catches, horizontal shading shows those with significantly low catches.

If the mean catch per section is 3·6888 the low threshold is 0. If the mean catch per section is less than 2·75, a zero catch in any one section cannot be considered significant, but two or more adjacent zeros may be, as shown at the top left-hand corner of the Table. This portion of the Table was calculated by temporarily considering the fly-round as made up of groups of 2, 3 or more sections, so that the mean catch per group would be 2, 3 or more times the mean catch per section. In the case in which the mean catch per section is 0·1, it is necessary to group 37 sections together to raise the mean catch to 3·6888, and therefore in this case 37 adjacent sections with zero catches would be considered a " significant low ".

This method can be applied only to crude unworked data (catch on a single day, or the totals for any convenient period) and not to worked data such as percentages, apparent densities, and means.

Summary.

The fly-round has for long been regarded as the most satisfactory way of following fluctuations in populations of tsetse flies (*Glossina*) and locating areas of concentration. It consists of a path cut through bush so as to traverse the principal vegetation communities and is divided into sections, corresponding to the latter, on each of which the flies are caught. A modification now widely used but not previously described in detail is termed a line transect or transect fly-round; this follows an arbitrary course along straight lines that may be orientated with regard to the topography and is divided into numerous short sections of

equal length terminating at posts at which flies are caught. In its simplest form it follows a straight course, but various patterns are used including an angular spiral. It facilitates the collection of quantitative data on tsetse density and the factors (such as vegetation) that affect it, and their analysis is possible in more detail than was the case when the fly-round was laid out according to a preconceived notion of vegetational relationships. This is illustrated by data from a fly-round at Shinyanga, Tanganyika, consisting of six sides, each of 2,000 yd., of two diagonally adjoining squares, that was divided originally into nine sections of varying lengths representing the floristic communities traversed, and subsequently into 120 sections each 100 yd. long. Comparison of the catches of non-teneral males of *G. swynnertoni* Aust. grouped according to the two methods emphasises the much greater detail provided by the second of them. The transect fly-round is easy to lay out and operate and is thought likely to be particularly useful in connection with reclamation work.

The effect of varying the section length was investigated for *G. swynnertoni* at Shinyanga, *G. pallidipes* Aust. in Nyanza Province, Kenya, and *G. austeni* Newst. in Zanzibar. With the first, progressively fewer flies of all categories except teneral males were caught as the section length was increased progressively from 50 to 200 yd.; with the other species a similar tendency was apparent, but not significant. The results emphasise a point long recognised but often neglected, that data from fly-rounds reflect, in part, the reaction of tsetse populations to the behaviour of the catching party. That this reaction, termed the availability, is itself inconstant is shown by catches of *G. pallidipes* on a fly-round done daily for a month, in which differences between catches on consecutive days, sometimes exceeding 3 : 1, must represent changes in availability, not in absolute population.

Data from the transect fly-round can be analysed so as to indicate sections where the catches deviate significantly from those expected on the assumption that they are distributed according to a Poisson series, and where there may thus be presumed to be areas of concentration of the population, or the reverse. A Table is provided to facilitate such analysis.

Acknowledgements.

We are indebted to Mr. W. H. Potts for helpful advice.

References.

Buxton, P. A. (1955). The natural history of tsetse flies.—*Mem. Lond. Sch. Hyg. trop. Med.* no. 10, 816 pp.

Harrison, H. (1936). The Shinyanga game experiment: a few of the early observations.—*J. Anim. Ecol.* **5** pp. 271–293.

Jackson, C. H. N. (1937). Some new methods in the study of *Glossina morsitans*.—*Proc. zool. Soc. Lond.* **1936** pp. 811–896.

Jackson, C. H. N. (1955). The pattern of *Glossina morsitans* communities.—*Bull. ent. Res.* **46** pp. 517–530.

Lloyd, Ll., Johnson, W. B. & Rawson, P. H. (1927). Experiments in the control of tsetse-fly.—*Bull. ent. Res.* **17** pp. 423–455.

Morison, C. G. T., Hoyle, A. C. & Hope-Simpson, J. F. (1948). Tropical soil-vegetation catenas and mosaics. A study in the south-western part of the Anglo-Egyptian Sudan.—*J. Ecol.* **36** pp. 1–84.

POTTS, W. H. (1930). A contribution to the study of numbers of tsetse fly (*Glossina morsitans* Westw.) by quantitative methods.—*S. Afr. J. Sci.* **27** pp. 491–497.

TANSLEY, A. G. & CHIPP, T. F. (1926). Aims and methods in the study of vegetation.—383 pp. London, Brit. Emp. Veg. Comm. & Crown Agents.

© Commonwealth Agricultural Bureaux, 1959.

STUDIES ON BEETLES OF THE FAMILY PTINIDAE.

XVII.—CONCLUSIONS AND ADDITIONAL REMARKS.

By R. W. Howe.

The purpose of this paper is to bring together the most important results of work with the 14 species of spider beetles (Ptinidae) that have been studied in this series and to discuss some matters which have not been adequately considered in the previous papers. References to these papers will be abbreviated to the author initials and number in the series, *e.g.*, the ninth paper in the series will be represented by H.B. 9 instead of Howe & Burges, 1953*a*, and the thirteenth by H.B. 13 instead of Howe & Bull, 1956.

Nomenclature of Species.

Hinton (1941) has produced an excellent key covering 24 species of spider beetles including all those of economic importance. A few additional species found occasionally in stored produce will also be mentioned in this paper. Many species have been misidentified fairly frequently and there have been a number of name changes since this series commenced. It is therefore necessary to comment on the names used here.

The family Ptinidae can be divided into two subfamilies, the Gibbiinae and the Ptininae. The former includes the two very characteristic storage genera *Mezium* Curtis and *Gibbium* Scopoli, to which must be added *Stethomezium*, which Hinton (1943*a*), in the original description, stated was closer to *Mezium* than any other genus. In spite of the very clear key and figures given by Fauvel (1883), there appears to have been a great deal of misidentification of the species of *Mezium*. *M. sulcatum* (F.) apparently does not occur in storage premises, but this name has been wrongly applied to specimens of the genus found indoors. The two species of this genus commonly recorded from stored produce have also been confused, especially in North America. Brown (1944) believes that *M. americanum* (Lap.) is restricted to the latitude of Florida and Texas. He considers that all records of this species for Canada are based on specimens of *M. affine* Boield., and this may be true also for most records of *M. americanum* from the north-eastern U.S.A., an area from which *M. affine* has been recorded. Hartnack's inference (1943, I, p. 225) that the two are forms of a single species appears unlikely. One other species of *Mezium*, *M. natalense* Pér., is recorded from stored produce only from southern Africa (Hinton, 1943*a*).

Zacher (1948) suggests that there may be confusion also over *Gibbium* species. The notes on antennal characters which he appends to his key to species of this genus should, if accurate, prevent *G. aequinoctiale* Boield. being confused with *G. psylloides* (Czenp.) or with *G. boieldieui* Lev.

Stethomezium at present is known by one species only, *S. squamosum* Hinton.

About half of the storage species included in the subfamily Ptininae fall into the genus *Ptinus*. This large heterogeneous genus is often divided into subgenera (Reitter, 1911, pp. 320–326; Yakobson, 1913, pp. 819–824) of which few have been adequately described or diagnosed. Reitter's key (1911, pp. 322–323) covers only six of these and their separation depends largely on the sexual dimorphism of body shape and on the presence or absence of a lobe on the penultimate joint of the tarsus, either in both sexes, one sex only or in neither sex. Some of the

subgenera, however, judging from the few species found in stored products, do group together related species. Most of the storage species of *Ptinus* belong to the subgenus *Ptinus*. They exhibit sexual dimorphism but have simple tarsi in both sexes. The species of this subgenus studied in this work include *P. fur* (L.), *P. pusillus* Sturm and *P. villiger* (Rttr.) as well as the species called *P. hirtellus* Sturm and *P. latro* F. in previous papers of this series.

Moore (1957) has shown that the species called *Ptinus hirtellus* should be known as *P. clavipes* Panzer. Moore, Woodroffe & Sanderson (1956) and Woodroffe (1958*a*) describe the biological relationship between this species and that called *P. latro* F. in these papers. Moore (*loc. cit.*) shows that *P. latro* F. is a synonym of *P. fur* (L.) and gives the name *P. clavipes* Panzer form *mobilis* to the insect we have studied. This insect may be regarded as a gynogenetic triploid form of *P. clavipes*. For convenience and clarity, in this paper it will be called *P. latro*, auct., and the name *P. latro* will not be used in any other sense.

P. clavipes and *P. latro*, auct., have been much confused in the past, as have other species of this subgenus. Thus Woodroffe (1954) records the misidentification of small male examples of *P. fur* as *P. subpilosus* Sturm. Earlier papers of this series (H. 14, H. 15) record muddles of identification of *P. pusillus*, *P. clavipes* and *P. subpilosus*. Hinton (1941) notes that *P. fur* and *P. pusillus* are often confused in collections. The discovery by Wise (1956) that the name *P. fur* has been frequently applied to *P. tectus* Boield. in New Zealand is most surprising, as the latter species should be placed in a different subgenus.

Other species of the subgenus *Ptinus* recorded from storage premises or animal nests are *P. agnatus* Fall, *P. bicinctus* Sturm, *P. gandolphei* Pic and *P. subpilosus*.

Several other subgenera exhibit a sexual dimorphism, including *Bruchoptinus* Rttr., *Pseudoptinus* Rttr., and *Cyphoderes* Muls. In *Bruchoptinus*, which includes *Ptinus rufipes* Ol., the penultimate segment of the tarsus is lobed in both sexes. In *Pseudoptinus*, which includes *P. lichenum* Marsham and *P. coarcticollis* Sturm, Reitter (1911, pp. 320–326) states in his key that this segment is lobed only in the male. Hinton (1941) evidently does not accept this tarsal character because he omits it from his list of sex differences in *P. lichenum*. For this species he states: "Tarsi with apex of fourth segment feebly dilated" whereas for *P. rufipes* he describes this segment as broadly dilated. *Cyphoderes* is characterised by two well-defined tomentose cushions and two gibbosities on the pronotum. It is represented in warehouses by *P. raptor* Sturm and *P. japonicus* Rttr.

In the subgenus *Gynopterus* Muls. (= *Ptinobruchus* Rttr.) there are only minor differences between the sexes; slight differences of the antennae in *P. californicus* Pic and *P. sexpunctatus* Panz., for instance. *P. exulans* Erichs. and *P. vaulogeri* Pic belong to this subgenus in which Yakobson (1913, pp. 819–824) also places *P. palliatus* Perris. Günther (1951) points out that the females of *Gynopterus* can be separated from those of other subgenera by the parallel-sided elytra and that males can be distinguished because of their short antennae. Hatch (1933) also places *P. tectus* in *Gynopterus* and claims that earlier workers were in error in placing it either in the subgenus *Ptinus* or in *Pseudobruchus* Pic. The similar form of the elytra in the two sexes and the short antennae are not sufficient justification for including *P. tectus* with species as different from it as *P. sexpunctatus*, and since it clearly does not belong in the subgenus *Ptinus*, it may perhaps be correctly placed in *Pseudobruchus* which has no other representatives in stored products. Certainly *P. tectus* merits a different subgenus from any other species considered here.

Many of the remaining species of spider beetles belong to the old genus *Niptus* Boield., which was split into a number of subgenera which are now accepted as genera, *e.g.*, *Tipnus* Thoms., *Pseudeurostus* Heyd., *Paraniptus* Kies. *Tipnus* is represented in storage premises by one species, *T. unicolor* (Pill. & Mitt.). Brown

(1940) considers that the generic name *Epauloccus* Muls. should be used but the name *Tipnus* will be retained in this paper. *Pseudeurostus* is also represented in storage premises by a single species *P. hilleri* (Rttr.). This species was originally referred in this series to the genus *Eurostus* Muls. but this name is preoccupied in the Heteroptera. The remaining species which will be mentioned in this paper are *Paraniptus globulus* (Ill.), *Niptus hololeucus* (Fald.), *N. ventriculus* Lec., *Trigonogenius globulus* Sol., *Sphaericus gibboides* (Boield.) and *S. brasiliensis* (Pic).

Wings of Spider Beetles.

Functional wings are present in warehouse spider beetles only in the genus *Ptinus s.l.* In the subgenus *Gynopterus* (*i.e.*, *P. sexpunctatus*, *P. californicus*), both sexes are fully winged and fly actively. In the subgenus *Ptinus*, most species are fully winged in the male (*P. fur*, *P. clavipes*, *P. villiger*) but, in the female, wings are reduced to tiny vestiges. In *P. pusillus*, the male wings are similarly reduced. The only evidence of flight by the winged males of the subgenus *Ptinus* is given by Woodroffe (1953, p. 760) who observed flight once in *P. fur*. In *P. tectus*, which as has already been mentioned, should perhaps be placed in the subgenus *Pseudobruchus*, the wings may vary from the complete to the vestigial with a wide variety of intermediate sizes including individuals with wings of unequal size (H.B. 9; Waddington, 1942). There is no record of flight in this species even among the small proportion that are fully winged. The wing character in *P. tectus* is probably genetically controlled but the mechanism is complex. In the other species associated with stored products there are no true wing vestiges. The species which have been examined are all the GIBBIINAE—*Gibbium psylloides*, *Mezium affine*, *M. americanum*, and *Stethomezium squamosum*; and the PTININAE other than *Ptinus s.l.*—*Niptus hololeucus*, *Tipnus unicolor*, *Pseudeurostus hilleri* and *Trigonogenius globulus*. The metathorax in these species, however, is often slightly evaginated on each side at the point where a wing would arise.

Larvae of Spider Beetles.

Böving (1956) justified the acceptance of the PTINIDAE as a family on larval characters and so reinforces their separation from the ANOBIIDAE on the basis of adult morphology.

A key to the larvae of many species of warehouse spider beetles was constructed by Manton (1945). Hall & Howe (1953) added further species to the key. Böving (1956) has described the larva of *Ptinus californicus* and Mathur (1956) has given a fuller description of that of *Gibbium psylloides*. It is thus possible to classify the storage species of the group on larval characteristics and compare the conclusion reached with those based on adults.

Larval morphology supports the close relationship of *Gibbium psylloides* to *Mezium affine*, but *Stethomezium squamosum* does not bear the two strong setae on the prementum which distinguish these two species from the others studied (Hall & Howe, 1953). Of the larvae of *Ptinus* spp. examined by Manton (1945) and by Hall & Howe (1953), *P. fur*, *P. clavipes*, *P. latro*, auct., *P. pusillus*, *P. villiger* (*i.c.*, subgenus *Ptinus*) and *P.* (*Cyphoderes*) *raptor* all have a large U-shaped anal sclerite, whilst in *P.* (*Gynopterus*) *sexpunctatus* and *P.* (*Pseudobruchus*) *tectus* the arms of this sclerite are shortened as in *P. californicus* (Böving, 1956), another species in the subgenus *Gynopterus*. *Niptus hololeucus* and *Pseudeurostus hilleri* resemble one another in lacking the empodial lobe on the legs and in *Tipnus unicolor* this lobe is small and ill-defined. In general, therefore, larval characters lead to a grouping which is very similar to that based on adults.

TABLE I.

World distribution of spider beetles which may be found in stored food and storage premises.

Species	Europe	Asia	Africa	America	Australasia
Gibbium aequinoctiale (circum-tropical, Zacher 48)	S. France (Yakobson)	Sumatra (Kalshoven 38) Syria, Persia, Assam & N. China (Yakobson)	Egypt (Zacher 48) Canary Is. (Boieldieu)	Cuba & Colombia (Boieldieu) America (Blackwelder) Mexico (Lepesme)	New Caledonia (Yakobson)
G. boieldieui	Russia & Europe (Hinton 41) Ukraine (Obraztsov) Transcaucasia (Yakobson)	Persia (Yakobson) Malay Archipelago (Hinton 41) Turkey (Yakobson)			
G. psylloides	Britain, Ireland (O'Farrell & B.) France (Pic) Germany (Reitter) Belgium, Holland & Denmark (Yakobson) Mediterranean (Zacher 38) Poland & Transcaucasia (Yakobson)	Japan (Fauvel 89) S. Asia from Arabia to Ceylon & India (Yakobson) Korea & Philippines (Yakobson)	Egypt (Zacher 38) Nigeria (Cotterell) Angola, Portuguese Guinea (Baeta Neves & others) Algeria & Madeira (Yakobson)	U.S.A. (Fauvel 89) Mexico, Cuba & W. Indies (Blackwelder)	Hawaii (Zimmerman)
Mezium affine (see H.B. 10)	Britain France (Pic) Germany (Reitter) Mediterranean (Zacher 38) Eastern Europe (Yakobson) & Transcaucasia (Yakobson)		North Africa (Hinton 41) Egypt (Zacher 48)	British Columbia (Follwell ; Hopping) East Canada (Brown 44) California (Linsley 44) East U.S.A. (Hubbard) Iowa (unpubl.)	N.Z. (North Island) (Wise)
M. americanum	Mediterranean (Yakobson)		Morocco, Madeira & Canary Is. (Yakobson)	Washington (Hatch 53) Texas & Florida (Brown 44) Chile (Boieldieu) Argentine, Peru (Blackwelder)	Hawaii (Zimmerman)
M. natalense			S. Africa & S. Rhodesia (Hinton 43*a*)		
Stethomezium squamosum			Egypt & S. Africa (Hinton 43*a*)		
Sphaericus brasiliensis				Brazil (Zacher 48)	
S. gibboides	Germany, France & Italy (Fauvel 89) Portugal (Baeta Neves & others) Mediterranean (Yakobson)		Algeria (Fauvel 89)	British Columbia (Spencer) California (Schwarz)	

Species	Europe	Asia	Africa	America	Australasia
Trigonogenius globulus ..	Britain Ireland (Beirne) Germany (Weidner) Finland (Vappula)		Africa (Hinton 41)	British Columbia (Follwell) Washington (Brown 40) Oregon (Fall) California (Linsley & Mich.) N.Y. (Brown 40) Columbia, Peru, Chile & Argentine (Blackwelder)	N.Z. (Wise) Tasmania (Hinton 41) Australia (Lepesme)
Tipnus unicolor	Britain Ireland (Beirne ; O'Farrell & B.) France (Pic) Germany (Reitter) Northern & eastern Europe Mediterranean & Faroes (Yakobson) Transcaucasia (Hinton 41)			N. Brunswick & N. Scotia (Brown 40)	
Niptus hololeucus	Britain Ireland (Beirne ; O'Farrell & B.) Northern, central & eastern Europe (Reitter, Pic, Hellén, Yakobson) Central Italy & Transcaucasia (Yakobson)	Asia Minor (Yakobson) Shanghai (Yakobson)		British Columbia Alberta, Ontario, Quebec, N. Brunswick & N. Scotia (Brown 40) Montana (Brown 40) Massachusetts (Gibson) S. America (Zacher 38)	Tasmania (Yakobson)
Paraniptus globulus ..	Germany (Zacher 48) Iberia (Yakobson)				
Pseudeurostus hilleri ..	Britain Ireland (O'Farrell & B.) Germany (Zacher 48)	Japan (Kiritani)		British Columbia, Ontario, Quebec & New Brunswick (Brown 40)	
Ptinus bicinctus	France (Pic) Germany (Reitter) Finland (Hellén) Norway (Munster) Most of Europe (Yakobson)		North Africa (Hinton 41) N. Nigeria (Howe 52) Algeria (Yakobson)	British Columbia (Follwell) Ontario (Brown 40) Massachusetts & Nebraska (Brown 40) Iowa (unpubl.)	
Ptinus clavipes and *P. latro*, auct. (see H.15)	Britain Ireland (O'Farrell & B.) All Europe south of Baltic (Yakobson)	Asia (Zacher 38) Persia & Asia Minor (Yakobson)	Africa & Madagascar (Lepesme) Algeria, Tunis, Madeira, Canary Is. & Azores (Yakobson)	British Columbia (Follwell) Ontario, Quebec & Nova Scotia (Brown 40) U.S.A. (N.Y. to N.M.) (Fall) Washington (Hatch 53) Oregon (unpubl.) California (Linsley & Mich.) Guatemala (Blackwelder)	N.Z. (North Island) (Wise) Hawaii (Zimmerman) New Caledonia (Yakobson)

TABLE I.—*continued*.

Species	Europe	Asia	Africa	America	Australasia
Ptinus fur	Britain Ireland (Beirne) Northern, central & eastern Europe (Pic, Reitter, Vappula, Munster, Yakobson) Faroes (Yakobson) Cyprus (Morris) Portugal (Baeta Neves & others)	Asia Minor, Mongolia, Siberia & Kamchatka (Yakobson) Japan (Hirose)	Algeria (Yakobson)	Alaska (Fall) Southern Canada (Brown 40) U.S.A. (Fall)	N.Z. (South Island) (Wise)
Ptinus gandolphei				California (Linsley & Mich.)	
Ptinus pusillus (see H.14)	Britain Germany (Reitter) Mediterranean, western & eastern Europe south of Baltic (Yakobson)	Asia Minor (Yakobson)			
Ptinus villiger (see H.B.11)	Germany (Reitter) Silesia (Zacher 48) Finland (Hellén) Norway (Munster) Central & north eastern Europe (Yakobson)	Siberia (Zacher 38) Caucasus (Zacher 38)		Canada (Brown 40) Northern U.S.A. (Fall)	
Ptinus californicus				British Columbia, Utah, Nevada & Colorado (Fall) California (Linsley & Mich.)	
Ptinus exulans	Holland (Everts) Germany (Reitter) S. Europe (Yakobson)	Asia (Hinton 41)			Australia (Rayment) Tasmania (Hinton 41)
Ptinus sexpunctatus	Britain France (Bedel) Germany (Braune) Belgium (Maréchal 29) Russia, Scandinavia, Mediterranean & Balkans (Yakobson) Norway (Munster) Finland (Hellén)				

Species	Europe	Asia	Africa	America	Australasia
Ptinus japonicus		Japan (Kiritani) China, Amur & Sikkim (Hinton 41) Bokhara (Yakobson)			
Ptinus raptor	Germany (Reitter) Finland (Hellén) Europe & Russia (Yakobson)	Amur (Hinton 41)		British Columbia (Follwell) Ontario, Quebec, N. Brunswick, N. Scotia & Newfoundland (Brown 40) Maine (Brown 40) New York (Schaeffer)	
Ptinus rufipes	Europe (Hinton 41)				
Ptinus tectus .. .. (see H.B.9)	Britain Iceland (H.B.9) Ireland Northern, central & eastern Europe (Lepesme, Zacher 48, Brinck, Hellén, Shapiro)		Kenya (H.B.9) (not established)	Alaska (Hatch 43) British Columbia (Spencer) Ontario, N. Brunswick & N. Scotia (Brown 40) Washington (Hatch 33) California (Essig) Oregon (unpubl.) Falklands & Tierra del Fuego (Hatch 33)	N.Z. Tasmania Melbourne (H.B.9) (doubtfully established) S. Georgia (Brinck)

World Distribution of the Spider Beetles of Storage Premises.

Since the distribution of some of the species considered in the earlier papers of the series was given only sketchily, the distribution of all species is discussed here with special reference to those species that occur in Britain. The various countries from which each species has been recorded are given in Table I with a reference to a published record for each area. The accuracy of the Table depends, of course, on the reliability of the identifications on which these records are based, and account has been taken of the errors of identification quoted earlier. The records of *Gibbium psylloides* for Egypt are taken as accurate in spite of Zacher's suggestion (1948) that they may be *G. acquinoctiale*, since I have seen specimens of the former species collected there. Zacher (1954) is in error in suggesting that *Stethomezium squamosum* is established in Britain. This species has not yet been recorded from commercial storage outside South Africa.

In our discussion of the distribution of *Ptinus tectus* (H.B. 9, p. 463) the first record of this species in North America was mistakenly attributed to Wilson (1915). In fact, the earliest North American discovery was in 1926 in Prince Rupert, British Columbia, where it was found in devastating numbers on fishmeal (Spencer, 1942). Hatch (1933) gives the first record for the U.S.A. *Ptinus tectus* is generally supposed to have originated from Tasmania, but Braune (1943, p. 548) gives reasons for doubting this. The species was described by Boieldieu (1856) from specimens collected in Tasmania but was not found in the heavily collected British Isles until nearly 40 years later, spreading to the European mainland still later. Evans, in his book on Tasmanian insect pests (1943, p. 143), states " it is possible, though not certain, that this is a native insect ". Recently, Wise (1956) pointed out that *P. tectus* had been collected in New Zealand by Wakefield in 1874, some 20 years before its discovery in Britain, but had been determined as *P. fur*, and that this error had been repeated several times during the following 50 years. From Wakefield's paper (1874) it appears that his specimens were named for him in England. Wise, however, still mentions it as an " introduced species ". Broun (1914, p. 195) states that " the widespread *Ptinus fur* and the Tasmanian *P. tectus* have been found at Methven by Mr. Hall feeding (sic) on the common laurel shrub ". This remark shows that not all the records of *P. fur* can be referred to *P. tectus* and that *P. fur* has been taken in the South Island of New Zealand. Although this is an outdoor record of *P. tectus* and *P. fur* not obviously associated with stored produce, it cannot be taken as showing that the species were established in the area. The specimen(s) of *P. tectus* were probably identified at the British Museum (Champion, 1913) which may account for Broun's reference to the species as Tasmanian. I believe the species originated in the southern hemisphere and spread to Europe when fast sea transport enabled the species to survive the passage through the tropics.

Species which are closely associated with commercial produce are very liable to be spread by trade and to become established in the climatically favourable areas they reach. There are numerous accounts, for instance, of the spread of *Niptus hololeucus* through Europe (*e.g.*, Kolbe, 1889; Zacher, 1939), possibly because it is a striking, easily recognised insect. The species which are restricted in distribution are those which are seldom associated with stored produce or those which cannot become established in competition with the species already present in any new area into which they are introduced.

Many spider beetles are restricted to cool and damp areas. These species have temperature optima at 25°C. or below and cannot colonise tropical countries (*e.g.*, *Niptus hololeucus*, *Pseudeurostus hilleri*, *Trigonogenius globulus* (H.B. 7); *Tipnus unicolor* (H. 12); *Ptinus tectus* (H.B. 9); *P. villiger* (H.B. 11); and *P. pusillus* (H. 14)). Other species have higher optima or can tolerate higher temperatures and are found in the tropics or sub-tropics (*e.g.*, *Gibbium psylloides*, *Stethomezium squamosum* (H.B. 7); *Mezium affine* (H.B. 10), *Ptinus fur* (H.B. 6); *P. clavipes*

(H. 15), and *P. latro*, auct. (H. 16)). With the possible exception of *Stethomezium squamosum*, all of the species of warehouse spider beetles studied are resistant to the coldest British weather (Solomon & Adamson, 1955), and this is reflected by the extension of the range of all the species into cool temperate regions and by their establishment in Britain when introduced.

Species which have been recorded by early British authors are: *Gibbium psylloides* (cited by Curtis (1831) as *G. scotias* Ol., by Stephens (1829 & 1839) as *G. scotias* F.): *Mezium affine* (cited by Curtis (1828), Stephens (1829 & 1839) as *M. sulcatum* F.): *Ptinus palliatus* (cited by Curtis (1837) as *P. germanus* L. and *P. rufipes* F.; by Stephens (1829 & 1839) as *P. germanus* Ol. and *P. rufipes* F.): *Ptinus sexpunctatus* Panz. (cited by Curtis (1837) as *P. sexpunctatus* F.; by Stephens (1829 (as a synonym of *P. muscorum* Leach) & 1839)): *Ptinus fur* (cited by Curtis (1837); Stephens (1829 & 1839)): *Ptinus lichenum* (cited by Curtis (1837); Stephens (1829 & 1839); by Stephens (1829) also as *P. similis* Marsham): *Tipnus unicolor* (cited by Curtis (1837) and Stephens (1829 & 1839) as *P. crenatus* F.; by Stephens (1829) also as *P. cerevisiae* Marsham).

From the figure given by Curtis (1828) it is clear that the *Mezium* is *M. affine*. He remarked that it was not uncommon in houses in London but was apparently unknown on the continent. Wollaston (1862) considered that the *Mezium* then found in central and southern Europe was constantly being imported and that the Canary Islands species were indigenous. Fauvel (1883) also considered that *Mezium* spp. originated in warm countries and spread to Europe. Curtis (1831) thought that *Gibbium psylloides* was an introduced species though it was known from houses in southern Europe, and was considered by Fauvel (1883) to be well established. Hence two of the seven spider beetles known in Britain by 1830 had been imported; two, *P. lichenum* and *P. palliatus*, were recorded from old posts and three, *P. fur*, *Tipnus unicolor* and *P. sexpunctatus*, from old houses. These situations suggest that these five species were native to Britain. Curtis (1837) stated that *P. fur* was common. *T. unicolor* was presumably not uncommon for it is the only spider beetle mentioned (as *P. crenatus*) in the 1883 edition of Curtis' "Farm insects". Although Curtis (1837) described *P. sexpunctatus* as "frequently destructive in houses living in wood and furniture and sometimes in museums," he clearly regarded it as a rarity.

Although not included in these lists, *Niptus hololeucus* had been imported into London (Bainbridge, 1837) and was included by Rye (1866) and Cox (1874), both of whom also included *Ptinus latro*, auct., but excluded *P. rufipes* as a distinct name. Cox also added *P. clavipes* (as *P. testaceus* Ol.) and *P. subpilosus*. The latter species is not associated with commerce and is presumably a native species. *P. clavipes*, recognised by Sharp (1873), and *P. latro*, auct., were probably imported around the middle of the century, although identifying them has been so difficult that records of many species of *Ptinus* are suspect (see Pool, 1915, Donisthorpe, 1941). Fowler (1890) included them as imported species which could not be regarded as established, along with another species, *P. pilosus* Müll., which has not since established itself. Fowler listed nine species, six native and three imported, plus these three doubtful species. *P. fur* was still the most common species but Fowler commented that *Niptus hololeucus* was "generally distributed and common, and had gradually spread and established itself even in the remotest country villages". The other four storage species were described as rare (*Gibbium psylloides*), local, not common (*Tipnus unicolor*), or not common (*Ptinus sexpunctatus*, *Mezium affine*). He noted that *Ptinus sexpunctatus* was "said to have been taken in a humble bee's nest in some numbers" but the association of this species with bees' nests noted so often on the continent (*e.g.*, Azambre, 1855) was not recorded in Britain until 1919 (Morley).

Three further species were introduced in the next few years and all became established. *Ptinus tectus* was first found in 1892 (Chitty, 1904), *Trigonogenius*

globulus in 1900 (Tomlin, 1900), and *Ptinus pusillus* was recorded by Donisthorpe (1906). All were included in the supplementary list of Fowler & Donisthorpe in 1913, by which time *P. tectus* had been found widely. Donisthorpe (1931) reported the import of *Ptinus exulans* but this species failed to become established. *Pseudeurostus hilleri* was first found in Britain in 1939 (Howe, 1940) and has spread widely to become established locally. Six years earlier it had been found in Germany (Zacher, 1938) but there is no evidence that it is established there. Hinton (1941) listed 16 spider beetles of economic importance (including *P. exulans* and *P. subpilosus* but omitting *P. sexpunctatus*) and three non-economic species (*P. palliatus*, *P. lichenum*, *P. sexpunctatus*) as recorded from Britain. In 1943*a*, he described *Stethomezium squamosum* from material stored in a museum, but this cannot be considered as an established British species.

Today, *Ptinus tectus* is undoubtedly the most common species in Britain, *Niptus hololeucus* is local and often very abundant; *P. fur* widespread but not common, *Trigonogenius globulus* and *Pseudeurostus hilleri* local and not common, and all the other storage species fairly rare. *Ptinus clavipes*, *P. latro*, auct., and *P. pusillus* tend to be found together. *Tipnus unicolor* is commoner in the north; *P. pusillus* is commoner in the south. *Mezium affine* is probably the rarest species in Britain. Single adults of *P. sexpunctatus* are frequently found drinking in wash-basins. In recent years *P. villiger* and *P. raptor* (Freeman, 1950) have been found on imported produce; and, since then, *Mezium americanum* has been intercepted at British ports.

Habitats and Food Habits of Spider Beetles.

Spider beetles are mainly scavengers and many species will feed equally readily on plant or animal materials. Consequently they can very easily become pests of stored goods. Many species are closely associated with the nests or excrement of other animal species, and other spider beetles are found in dead or decaying wood. Xambeu (1894), for instance, mentions species living in sheep droppings scattered in pastures and others living in the dead branches of trees. Several species have been mentioned as living in caves, *Mezium americanum* in the Canary Islands (Wollaston, 1862), *Tipnus unicolor* breeding in guano in Belgium (Leruth, 1935) and central Europe (Pax & Maschke, 1935), *Ptinus clavipes* and *Mezium affine* in guano in Algeria (Jeannel, 1909). No doubt some species of spider beetles were introduced into primitive stores in the wood used to construct them, while others were attracted by the ample food supply kept in conditions suitable for the insect. The food supply would also have attracted certain mammals and birds, some of which nested in the store and provided extra amenities for spider beetles.

Many spider beetles are native to semi-desert areas. The present series of papers and the work of Braune (1943), however, show that the storage species must have access to drinking water if they are to lay eggs and multiply. If the desert species also need water, then they are most likely to obtain a sure supply in the homes of rodents, bats, birds or insects where urine, moist excrement, honey or some such fluid may be provided. In addition, food will probably be available in excrement, seeds, pollen or carrion. In desert conditions or in the shelter of nests in moister places, the larval foodstuff, be it leaf, seed, excrement or carrion, is not likely to rot before larval feeding is complete. Spider beetles are normally found associated with animals nesting under shelter or in holes—very frequently with the species like rats and birds that invade storage premises—but not with animals, such as moles, nesting in burrows or exposed situations. Woodroffe (1953) discusses the characteristics of the dry nest environment and its influence on the nest fauna. Pence (1955) comments on the rapid invasion by an unidentified spider beetle of a house in what is presumably a newly developed housing estate in a desert area in Inyokern County, California.

TABLE II.

Spider beetles associated with animal nests.

Species	Insect nests	Birds' nests	Mammal nests
Mezium affine	—	Pigeon (W.) Sparrow (W.)	Bat (W.56) Rat (L.44) ,, (Hubbard)* ,, (Pescop)*
M. americanum	—	Sparrow (Mallis) ,, (Zimmerman)	Rat (Mallis)
Gibbium psylloides	—	—	Kusu rat (Briscoe)
Trigonogenius globulus	—	Pigeon (W.)	—
Tipnus unicolor	Humble bee (Weid.)	Birds (Fowler) House martin (Hinton 41) Pigeon (Rye 73) ,, (Weid.) Thrush (Heselhaus 15)	Rodent (Xambeu 94)
Niptus hololeucus	*Dolichovespula* (Tuck 97) †*Formica* (Reh) *Vespa* (Weid.) Hives (L.42)	Birds (Weid.) Jackdaw (Lloyd) ,, (W.) Pigeon (Jeannel) Swallow (Jeannel) ,, (K.)	Rat (Woodroffe u.)
N. ventriculus ..	—	—	Kangaroo rat (Brown u.) Wood rat (Brown u.)
Pseudeurostus hilleri	—	Pigeon (W.)	—
Ptinus agnatus	—	—	Wood rat (Davis)
P. bicinctus ..	—	Pigeon (Everts) ,, (Heselhaus 14, 15)	—
P. clavipes ..	*Sceliphron* (L.44)	Birds (K.) Great tit (K.) Pigeon (Chittenden) ,, (Girard) ,, (Xambeu 94) Poultry (Chittenden) ,, (Xambeu 94) Sparrow (McAtee) ,, (K., K.39) ,, (W.) Starling (Gebien) ,, (Weid.) Swallow (Everts) ,, (K.) Tree sparrow (K.)	Rat (Pilate) Wood rat (Brown u.)
P. latro, auct.	—	Pigeon (Xambeu 94) Sparrow (Xambeu 94)	—
P. fur ..	*Apis* (Bartels) ,, (Hinton 43b) *Chelostoma* (Maréchal 33) *Osmia* (Enslin) ,, (Schmitt) *Vespa* (Bargagli) ,, (Butler) ,, (Husing) ,, (Tuck 96) *Vespula* (Braune) ,, (Tuck 96) Honeycomb (Weid.) [Spider (Auten)]	Birds (K., K.39) American robin (Dobroscky) Blackbird (Lehnert) Bluebird (McAtee) Chaffinch (N.) Great tit (K.) (N.) House martin (K.) (N.) ,, (Low) ,, (W. & Southgate) ,, (Székessy 48) Housewren (McAtee) Jackdaw (N.) (W.) Pigeon (Bickhardt) ,, (Falcoz) ,, (Gerhard) ,, (Heselhaus 14, 15) ,, (K.) (N.) ,, (Lehnert) ,, (Rye 73) ,, (Székessy 48) ,, (Woodroffe u.)	Bat (W.56) Rat (Pilate) Squirrel (Leleup)

TABLE II.—*continued.*

Species	Insect nests	Birds' nests	Mammal nests
P. fur (cont.) ..		Redstart (K.) Shelduck (W.) Sparrow (K.) ,, (W. & Southgate) Starling (Gebien) ,, (Weid.) ,, (Zacher 38) Swallow (Gebien) ,, (K.) ,, (Low) ,, (Resch) ,, (Székessy 48) ,, (Weid.) ,, (Zacher 38) Tawny owl (Spittle) Tit (Lengerken) Tree sparrow (K.) White stork (Szekessy 50) White wagtail (N.) ,, (Szekessy 48) Woodpecker (Lengerken)	
P. gandolphei ..	—	Barn owl (L.44)	—
P. pusillus ..	—	House martin (W.) Jackdaw (W.) Pigeon (W.) Sparrow (W.) Swallow (W.) †Pigeon or starling (Blair 30)	—
P. subpilosus ..	*Lasius* (Donisthorpe 27) ,, (Donisthorpe 41) ,, (Fowler) ,, (Fowler & Donisthorpe) ,, (Walker 20*b*)	—	Squirrel (Jansson)
P. villiger ..	—	Birds (Weid.) House martin (N.) Swift (N.)	
P. raptor ..	†with *Formica* (Munster) *Vespa* (Schaeffer) Beehives (Arnhart) ,, (Brassler)	—	—
P. californicus	*Anthophora* (L.44) *Osmia* (L. & MacSwain)	—	—
P. sexpunctatus	*Andrena* (Azambre) *Anthophora* (Hamm) *Bombus* (Fowler) *Chalicodoma* (Bargagli) ,, (Caillol) ,, (Redtenbacher) *Chelostoma* (Maneval) *Hoplitis* (Maneval) *Lasius* (Walker 20*a*, 20*b*) *Megachile* (Bedel) ,, (Maneval) *Osmia* (Ashe) ,, (Caillol) ,, (Chevalier) ,, (Enslin) ,, (Hamm) ,, (Maneval) ,, (Maréchal 29, 32) ,, (Morley) ,, (Nicolas)	House martin (W.) Sparrow (Blair 24) ,, (W.)	—
P. vaulogeri ..	*Osmia* (Cros)	—	—
P. exulans ..	deserted hives (Rayment)	—	—
P. coarcticollis ..	with ants (Koltze)	Owl (Meeuse)	—
P. rufipes ..	—	Birds (K.) Hooded crow (N.) Stock dove (N.)	—

TABLE II.—*continued.*

Species	Insect nests	Birds' nests	Mammal nests
P. tectus ..	*Vespula* (Weid.)	Birds (K.) (Zacher 39) Blackbird (Lehnert) Great tit (K., K.39) House martin (K.) ,, (W. & Southgate) Pigeon (Donisthorpe 47) ,, (O'Mahony) ,, (W.) Redstart (K.) Sparrow (K., K.39) (W.) ,, (W. & Southgate) Swift (K.51) Tree sparrow (K.) ,, (Weid.)	Bat (W.56)
Unidentified Ptinids .	Bees (Friese)	Blue tit (K.) Martin (Cornelius) Swallow (Cornelius) Swift (Cornelius)	—

Abbreviations : *—*M. americanum* in originals K. =Kemper 1938 N. =Nordberg Weid. =Weidner
†—Association not proved L. =Linsley W. =Woodroffe 1953 u. =unpublished

There are very many published records of spider beetles associated with the nests of animals. Table II is as complete a list * of original records as I am able to compile. They are mainly from Britain, France, Germany and the U.S.A. Of the 14 species examined in the present series of papers, the only one missing from this list is *Stethomezium squamosum*, which has not yet invaded commercial storage except possibly in South Africa. Some of the recently introduced species, such as *Pseudeurostus hilleri*, which have gained entry into new countries on produce and must reach the nests from warehouses, have, as yet, seldom been found in nests. Certain species, such as *Ptinus sexpunctatus*, *P. californicus* and perhaps *P. exulans*, *P. raptor* and *P. vaulogeri*, are found mainly in the nests of bees and seldom in other nests. Larvae of these species may require honey or pollen and where only poorer foods are available will grow more slowly and may even starve. *P. subpilosus* appears to be more or less restricted to rotten wood and ant nests. Lea (1905, 1910) mentions spider beetles that live in the nests of ants in Australia, and Crowson (1955, p. 79) points out that the two small families of myrmecophilous beetles, Gnostidae and Ectrephidae, are probably true Ptinids. The ecological conditions in the insect nests are probably similar in all the species and genera of bees and ants concerned, whereas there are great differences between the nests of various vertebrates. No spider beetle can be associated specifically with any species of bird or mammal, although certain nests may be especially attractive to certain species, *e.g.*, *P. tectus* to pigeon (Woodroffe, 1953). *P. fur* has been found in a wide variety of nests, both of vertebrates and arthropods.

Since it is difficult to determine precisely the validity of many of the literature records given in Table II, every record has been accepted in which association with a nest is stated or implied. Some of the records undoubtedly are accidental, for instance where a species has been introduced on nest-building material, but the vast majority will be due to the nest providing a favourable environment together with a food cache, faecal pellets, and animal remains.

Some of the records are due to spider beetles breeding in animal remains in deserted nests, and, in some instances, the record states that the nest examined was old. Thus Weidner (1952) found *Niptus hololeucus* and *Ptinus tectus* in

* An exhaustive list of insects found in birds' nests, including references which are obviously quoted from other papers, has been published by E. A. Hicks (1959).

year-old hornet and wasp nests, Schaeffer (1931) found *P. raptor* in a museum-exhibit wasp nest, and Rayment (1935) records *P. exulans* from deserted hives. There is also a possibility that spider-beetle larvae eat living insects. Braune (1943) states that he observed *P. sexpunctatus* eating healthy larvae of *P. fur*, and we have observed cannibalism (H.B. 9) in *P. tectus*.

One of the principal sources of food in nests and burrows is the excrement, which often contains semi-digested food material and provides a favourably high humidity. Spider-beetle larvae have often been found inside the faecal pellets of rodents. Because of this, Pescop (1953) suggests that the presence of Ptinids may be taken as an indicator of the probable presence of rats. This deduction can be carried too far, for in a warehouse containing ample food supplies, dampness is more likely to stimulate population growth than the presence of rat droppings. The species most commonly associated with rat droppings and other excreta are *P. clavipes* (Falcoz, 1914; Pergande, 1886; Pescop, 1953; Xambeu, 1894) including *P. latro*, auct. (Xambeu, 1894), *P. fur* (Bickhardt, 1911; Gerhard, 1909; Heselhaus, 1914; Hinton & Greenslade, 1943; Xambeu, 1898, pp. 11–12) and *Niptus hololeucus* (Falcoz, 1914; Vogel, 1929; Weidner, 1952). Salmond (1956) examined a flour mill in Scotland and found that *Niptus hololeucus* " is always close to rat and mouse droppings ". In the present work (H. 3), six species of spider beetle were found in a warehouse storing flour in which *P. tectus* was very abundant but only larvae of *N. hololeucus* were found inside rat droppings.

Another common ingredient of nests is hair or feathers. It is not clear how far keratin can be utilised, if at all, by spider beetles. Soiled woollens may be eaten for the contaminant, but there are some records in which it seems that clean wool or wool dust may actually serve as a nutrient for larvae. Woodroffe (1958*b*) has seen large breeding populations of both *Trigonogenius globulus* and *Niptus hololeucus* in refined woollen waste in a clothing factory. Wise (1956) gives a number of records from clothing fabric or wool warehouses, including one of damage to raw [dirty ?] wool by *P. tectus*. Wise, however, points out that he omits records from " clothes and carpets because it is not known that these beetles have caused damage ". In the laboratory, adults of *P. tectus* can damage clean knitting wool, but larvae do not survive thereon. Wandering fully fed larvae are able to bore through carpet and other fabric, into wood or even into lead, a habit which undoubtedly leads to some erroneous allegations of feeding.

Some species of spider beetle are typically found in dead wood but none is a pest of sound timber. Crowson (1955) considers that " a derivation of the family Ptinidae from some *Hedobia*-like type of Anobiidae would seem likely ", so it is natural that there has been some speculation as to whether certain species are true wood-borers. Crowson (1955, p. 79) states that " as far as is known no Ptinid is a true wood borer " and postulates that the loss of the wood-boring habit was a fundamental factor conditioning the divergence of the Ptinidae as a family. Picard (1919), however, states that the larvae of *P. lichenum* " perfore l'écorce et le bois sec [of fig] à la façon des *Anobium* ". The species characteristically found in dead wood (*e.g.*, *P. palliatus*) are probably primitive. Larvae of most storage species have been found boring into sound timber at some time, though it is unlikely that they were feeding (Shapiro, 1948). It is possible, however, that they can utilise friable decaying timber or the fungi, dead insects and other organic detritus in such a habitat.

The range of foodstuffs available to and used by spider beetles is very wide. It is remarkable, therefore, that *Pseudeurostus hilleri* and *Niptus hololeucus* were unable to complete their development on fishmeal in some laboratory experiments. These species did well on this foodstuff when yeast was added.

There is a number of records of spider beetles feeding in unusual foodstuffs or living in the apparent absence of food. For instance, Woodroffe (1953) comments

on the "peculiar preference" of *Niptus hololeucus* "for rubbish such as mortar rubble", a situation in which it has been found several times with little if any obvious food. Hartnack (1943, I, p. 206) states that adults of this species and of *Ptinus fur* (cited by the U.S. popular names of brass beetle and pilferer, respectively) are "omnivores which eat many things though they may be unable to digest them". Scott (1921) records *Trigonogenius globulus* breeding in argol, which is a crude potassium tartrate probably containing organic impurities. Beirne (1952) records this species breeding in crude tartaric acid and Hartley (1957) found adults of *P. tectus* and *Niptus hololeucus* in domestic tartaric acid but there was no evidence of breeding. Kemper (1956) found spider-beetle larvae feeding in holes in a wax candle.

Spider beetles have been recorded several times on tobacco or in tobacco warehouses (Escherich, 1914; Livingstone & Reed, 1936; Runner, 1919; Tenhet & Bare, 1951; Ustinov, 1932) and the suggestion made that they feed on tobacco. Most likely they breed principally on dead tobacco beetles and moths but they may utilise tobacco dust along with other organic débris present in warehouses.

Summing up, spider beetles in Britain include purely outdoor species, others confined to warehouses, and intermediate species which can live either indoors or out. *P. lichenum* and *P. palliatus* are always found in natural habitats in association with dead wood; *P. subpilosus* is always found in natural habitats but these include the nests of ants; *P. sexpunctatus* is principally found in the nests of bees but may be found in the nests of house martins—an atypical natural site—and in houses and storage premises. *P. fur* is most common in warehouses but may still be found in purely natural habitats such as the nest of the shelduck (Woodroffe, 1953), in fungi or faggots. No other spider beetle is found wild in Britain, not even *G. psylloides*, *M. affine* or *T. unicolor*, which could be found in houses over a hundred years ago. These and the more recently imported species are often found in nests but have been found only in nests built on or inside buildings and never in nests from the open country.

Damage done by Spider Beetles.

Significant damage by spider beetles occurs only when large populations are allowed to develop. Gunn & Knight (1945) were able to breed average-sized examples of *P. tectus* (about 3 mg.) on 30 mg. of flour. Since the largest spider beetles found in warehouses weigh only about 8 mg., 100 mg. of flour would be ample for the growth of any individual. The food value of even this small quantity would not be impaired unduly as not more than 20 mg. of the food would be metabolised. Taking 30 mg. as sufficient flour for the growth of a single example of *P. tectus* from egg to adult, one pound weight could produce 15,000 beetles. Thus the population of about one third of a million beetles present in a warehouse room (H. 3) would cause only about 20 lb. loss of weight, less than spillage and spoilage during storage and transport. The real damage caused by spider beetles is indirect. Flour and meals are contaminated with frass, fragments of dead insects and silk which are detectable but not easily removed. Cereal grains are spun together by the silk which is used to build the cocoon, and occasionally by the mucous threads produced by feeding larvae. Spider-beetle damage is easily recognised because larvae eat the bran coat unevenly from the grains.

The most obvious damage is caused by the fully fed larva wandering in search of a pupation site rather than by the feeding larva. They bore holes in textiles, in containers, whether of jute, linen, cellophane, plastic or cardboard, and may weaken them seriously. They build their cocoons in shallow depressions so that sacks, and cellophane packages inside cartons, can be covered by masses of silk cocoons. Outside the U.S.A., the cocoons on sacks are still tolerated, but if branded goods packed in cartons become infested, the manufacturer faces a severe

loss of reputation. Often the larva leaves the goods entirely to build its cocoon and then, if it fails to find a suitable depression, it will make one in a floor-board or wood surface or enlarge a crevice in the floor (Shapiro, 1948). Spider-beetle larvae can penetrate into somewhat harder materials, and there are several records of their boring into lead (Duffy, 1953).

The best guide to the damage caused by spider beetles is therefore the size of the population present. Populations grow most rapidly in dark, damp premises, in goods which are not disturbed, at temperatures of about 20°C.

Distribution of Spider Beetles in Premises.

If produce infested by spider beetles is introduced into storage premises the beetles quickly become established there if the building provides any cracks in which they can hide during daylight. Thereafter, any produce placed in the store in turn becomes infested. The principal factor controlling the distribution and spread of these beetles in warehouses is the behaviour of the adult. Both distribution of beetles in warehouses and adult behaviour have been studied for *Ptinus tectus*, and the results appear to be valid for other warehouse spider beetles. Adults are usually active at night (Ewer, 1943; H. 3), but in premises which are kept dark all day there are always active adults present. The amount of activity depends on temperature, but mass activity of spider beetles continues down to 3°C. and some individuals still walk about at 0°C. Gunn & Hopf (1942) showed that adult activity is affected by previous temperature experience so that a warm day could be expected to stimulate movement during the following night. They also showed that rapid changes of temperature induced movement. Bentley, Gunn & Ewer (1941) showed that activity is greatest at falling temperatures at about 10–15°C. The presence of food reduces activity as well as constituting an obstruction to free movement. Bentley (1944) found that the effects of humidity varied with the need of the beetles for water. In low humidities the beetles are at first inactive, thereby conserving their water, but as they get thirsty they become more active, which makes them more likely to discover a water supply if one is available.

Adult spider beetles will be very obvious in an infested warehouse on warm humid nights, but as the light increases at dawn the beetles will hide in the dark crevices of the floor or wall of the room, between sacks, in their ears or underneath débris. When produce is removed, the population in the warehouse structure is left behind and this will tend to infest the peripheral zone of the new produce stacked in the room. Produce, especially sacked goods, is an obstacle to free wandering of adult beetles, but those insects on sacks in the centre of a stack tend to move outwards. Movement is often easier near the outside of the stack where the packing is less tight. Insects outside the stack tend to move along the edge or on the free floor space and penetrate the bulk very little. The distribution of eggs and larvae is determined by the position of the adults, so a strongly peripheral distribution of spider beetles results. Also, the infestation of individual sacks is largely peripheral since eggs are laid through the sacking.

Spider beetles are often trapped in vessels such as jam jars or on insecticidal films during their nocturnal wandering. This trapping often draws attention to the occurrence of the golden spider beetle, *Niptus hololeucus*, in houses. Also, it leads to the suggestion, often erroneous, that certain insecticides irritate them and drive them from the cracks.

Parasites and Predators.

Warehouse spider beetles appear to be relatively free from natural enemies. Some of the few records of parasites and predators are based upon observations in cultures or in laboratory experiments. Spider beetles are probably vulnerable to

attack by any of the general beetle parasites and by any predator of suitable size found in warehouses.

The parasites recorded include the Bethylid, *Cephalonomia gallicola* (Ashm.), from *Ptinus fur* (Bridwell, 1919), also recorded as *C. xambeui* Giard, again from *P. fur* (Nielsen, 1932), and as *C. quadridentata* Duch. from *P. tectus* and *Niptus hololeucus* (van Emden, 1931); and the Pteromalids, *Dimachus discolor* (Wlk.), from *P. tectus* (Zacher, 1933), and *Lariophagus distinguendus* (Först.) from *P. fur* (Herold, 1933; Hüsing, 1935) and *P. tectus* (Kashef, 1956). Leonardi (1926) records a number of parasites of *P. fur* which can be accepted only with reserve; the Ichneumonid, *Cryptus ptinivorus* Rond., the Braconids, *Hecabolus sulcatus* Curt. and *Spathius exarator* (L.), as well as a Dryinid, which is presumably incorrect. The mites recorded from spider-beetle cultures include *Hypoaspis* sp. (Hickin, 1941), *Scius* (as *Scjus*) sp. (Zacher, 1928), *Cheyletus eruditus* (Schr.), *Pediculoides ventricosus* (Newp.) and *Blattisocius* (cited as *Typhlodromus*) *tinci-vorus* (Oudm.) (H.B. 6 & 9) which are predatory, and *Thyreophagus entomophagus* (Lab.), *Glycyphagus domesticus* (Deg.) and *G. destructor* (Schr.) which are not, but which are present in cultures in which many larvae die. Hickin (1946), however, suggests that when *Hoffmannophila pseudospretella* (Stut.) is present, *Ptinus tectus* and the mite, *T. entomophagus*, can co-exist in the same culture. Zacher (1928) records the spider, *Theridion familiare* Cambr., as an enemy of *N. hololeucus*.

Eichler (1939) records a gregarine disease of *N. hololeucus*. Non-pathogenic gregarines appear to be present in the gut of all warehouse spider beetles, and all seem to be vulnerable to the pathogenic species found in the body cavity. Cultures of *N. hololeucus* and *Trigonogenius globulus* have been attacked by an unidentified disease of bacterial or viral origin.

Culture Methods.

The maintenance of cultures of most warehouse spider beetles in the laboratory does not present much difficulty. Almost any stored food can be used as a culture medium, especially if dried powdered yeast is added to make up any vitamin deficiency. The food is best provided as a meal, and any material which is too oily to grind (*e.g.*, groundnuts) or too sugary to grind (*e.g.*, dried fruit) is unsatisfactory. Wheatfeed or wholemeal flour have proved to be adequate, but fishmeal or meatmeal may be used for some species, and a mixture of equal parts of wheatfeed and meatmeal will probably suit all species.

Cultures may be seeded with adults which can be transferred to new food at weekly intervals if many cultures are needed, or left for about three months on the same food if only a reserve stock culture is wanted. A group of 100–200 adults gives a satisfactory culture but it is usually easy to obtain a culture from 20 beetles or less, and preferable not to overcrowd the culture initially. It is essential to provide the adults with water either by placing them on moist filter paper when new cultures are prepared, or, if the adults are not often handled, by placing a drinking tube or "fountain" (Woodroffe, 1958*a*) in the culture. The best breeding temperature is about 20°C., but this can be varied according to the species and rate of growth required. Cultures should be kept at about 70 per cent. R.H. They are usually contained in jam jars closed by a porous textile held in place by rubber bands. The use of a filter paper sealed in place with paraffin wax was suggested by Dr. P. L. Robertson and has been developed by Miss E. M. Reynolds. This prevents the spread of mites and Psocids should any culture become contaminated.

Only two species have presented difficulty. The problem of *P. latro*, auct., was solved by the work of Moore, Woodroffe & Sanderson (1956) who are stated by Woodroffe (1958*a*) to have presumed that females of *P. latro*, auct., captured in the field would have been fertilised. A culture of such females produced

female progeny only, and in order to obtain progeny from these and subsequent generations, all of which comprised females only, it was necessary to provide males of *P. clavipes*. Since it appears, therefore, that there is no male of *P. latro*, auct., and unmated females do not lay viable eggs, this form can only be maintained by introducing males of *P. clavipes*, or with much less success, *P. pusillus* (Woodroffe, 1958*a*).

Difficulties in the breeding of *P. villiger* were not satisfactorily overcome. A limited number of larvae was bred through in each generation when the surface area of cultures was enlarged and the culture placed in a refrigerator for about two months at intervals of about six months. It seems possible that adult beetles are not fertile unless the full-grown larva, pupa or young adult experiences temperatures close to freezing point. A small culture has been maintained for eight years.

Linsley (1942) states that *P. californicus* can be reared readily on cornmeal and other cereal products although it has never been recorded as breeding outside the nests of bees. This is equally true of the European species, *P. sexpunctatus*, which also has never been recorded as breeding in warehouses although adults are found in houses and stores.

The Life-cycle.

All stages of the life-cycle of all spider beetles develop rather slowly in comparison with other storage insects, the shortest period for a complete generation in any species being about eight weeks. The shortest period for the hatching of the egg is about seven or eight days in *Ptinus tectus*, *P. sexpunctatus*, *Pseudeurostus hilleri*, *Gibbium psylloides* and *Mezium affine*, compared with less than three days in *Tribolium*. For *Tipnus unicolor* it is as much as 15 days and for *Ptinus fur* and *P. pusillus* 16 days. Normally, over 80 per cent. of eggs hatch, but freshly hatched larvae will puncture eggs in the absence of food and reduce the percentage hatch.

In all species there are normally three larval instars. The second is usually slightly longer than the first, and the third, including the prepupal period, usually two to three times as long as the first (Howe, 1943). The last instar forms the smallest proportion of the larval life in *G. psylloides* and the largest proportion in *P. tectus*. The effects of adverse constant conditions seem to be cumulative, prolonging the last instar more than the others. Thus, while the last instar comprises about 50–55 per cent. of the larval developmental period between 15 and 23°C., it increases to 60 per cent. at 25°C., and 70 per cent. at 11°C. Low humidity and poor foods induce similar increases. Another consequence of poor conditions is an increase in the number of instars for certain individuals, many of which die as larvae. One larva of *Trigonogenius globulus* (H.B. 7) had seven larval instars when fed on unsatisfactory food. Fishmeal is probably deficient in vitamins, for with most species up to 10 per cent. of larvae provided with this food had additional moults in satisfactory temperature and humidity conditions. On wheatfeed at 70 per cent. R.H. and moderate temperatures, the larva accounts for about 55 to 60 per cent. of the developmental period of those species which have a simple life-cycle, but at high and low temperatures this proportion increases to 65–70 per cent. Evidently the larval stage is more affected by adverse conditions than egg or pupa.

The duration of the pupal stage is broadly similar to that of the egg period at the same conditions for each species. The shortest pupal period was recorded for *Pseudeurostus hilleri*, 6½ days at 25°C. For *Ptinus tectus* the shortest was about nine days at 25°C.; for *P. sexpunctatus* at 30°C. the pupal period was just over seven days, and for *Mezium affine* it was eight days at 33°C. On the other hand, the shortest mean pupal period recorded for *P. fur* was 16 days.

In certain species it is clear that there is a small but definite and consistent sex difference in the duration of the pupal period, the male requiring somewhat less than a day extra. This has been observed in *P. clavipes*, *P. fur*, *P. pusillus* and *P. sexpunctatus*.

The adult, after transformation from the pupal stage, remains dormant in the cocoon and during this period the gonads usually mature. With a well-built cocoon in undisturbed conditions, for most species this dormant period is usually a little shorter than the pupal period. In all species the average weight of the female on emergence from the cocoon is greater than the average weight of the male.

The life-cycle of all the species of *Ptinus s.l.* except *P. tectus* is complicated by resting stages which also occur in laboratory experiments at constant temperature. With *P. tectus*, and with all the species of other Ptinid genera studied, there is no resting stage and in these insects the developmental period decreases with rising temperature up to an optimum, further rise of temperature being harmful. All stages of development are affected in a similar way (Table III). The effect of temperature on the other species of *Ptinus* studied is less simple, for somewhere in the 20–23°C. range there is a discontinuity, the exact placing of this critical temperature differing slightly between species. Above this critical temperature larvae develop quickly, whilst below they may show a very protracted development with a true diapause of the fully fed larvae (Table III). Near the critical point some larvae enter diapause and some do not. At higher temperatures, therefore, adults are formed in the larval cocoon much more quickly than at low temperatures. These adults, however, remain in the cocoon much longer than those bred at lower temperatures and as a result the total period from the laying of an egg to the emergence of the resulting adult varies somewhat irregularly with the temperature. The adult resting stage is not a true diapause, for simple removal of these adults from the cocoon is followed immediately by normal mating and oviposition.

These features affect the type of population of each species found in warehouses. *P. tectus*, for instance, may be found in any developmental stage at any time of year. *Niptus hololeucus*, *Pseudeurostus hilleri* and others are also likely to be present in any stage at any time, but the slower development of *N. hololeucus* restricts it to one generation a year instead of the two or even three possible for *Ptinus tectus*.

Braune (1943) gives an account of the life-cycles of five spider beetles of the genus *Ptinus* in Germany. He quotes figures, for instance, on the duration of the pupal period and the quiescent period spent by the adult in the cocoon. Whereas these data are given for *P. tectus* for most months of the year, similar data for the other species are restricted to a limited period, July and August for pupae, for example. This is true every year irrespective of the variations of weather and is due to the occurrence of resting stages overriding the effects of temperature. Emergence of the adult and the breaking of larval diapause of these species of *Ptinus* are probably both induced by small environmental changes which occur at such a time as to bring out the adults at a given season, irrespective of when the eggs were laid. Those individuals growing just too slowly to emerge in one year are enabled to wait until the more propitious time in the following year. In constant conditions, mortality of diapausing larvae is high, possibly due to the absence or weakness of the stimulus for ending the diapause. This absence of stimulus may artificially increase the diapausing period of those larvae which do eventually emerge in these experiments. The quiescent periods obtained in the laboratory agree quite well with the figures given for natural conditions by Braune (1943), except his data for *P. clavipes*. His figures for *P. latro*, auct.$_{\text{a}}$ and for *P. clavipes* are very different, even though it is evident that he could not distinguish these species with certainty.

TABLE III.

Larval developmental period and time spent in cocoon by quiescent adult for several spider beetles.

Species	Temp. (°C.)	Sex	No.	Larval period (days)	Adult in cocoon (days)
Ptinus pusillus (on wheatfeed)	25	♀	9	53	141
		♂	10	51	110
	22·5	♀	7	54	137
		♂	10	56	89
		♂	1	313	49
	20	♀	6	289	109
		♀	4	446	56
		♂	6	384	76
	17·5	♀	12	364	41
		♂	5	353	26
P. fur (on fishmeal)	23	♀	15	65	49
		♂	2	63	40
		♂	10	313	47
(on wheatfeed)	20	♀	11	67	60
		♀	2	407	41
		♂	9	61	56
		♂	2	292	45
P. sexpunctatus (on wheatfeed)	20	♀	7	57	142
		♂	4	59	101
		♂	2	218	49
(on fishmeal)	20	♀	3	279	39
		♀	3	128	69
		♂	3	397	25
		♂	2	164	38
Mezium affine (on wheatfeed)	25	—	10	48	8
	20	—	15	84	12
Trigonogenius globulus (on wheatfeed)	25	—	20	42	8
	20	—	50	56	10
Ptinus tectus (on fishmeal)	25	—	75	44	6
	23	—	20	50	8
	21	—	85	60	10
	15	—	60	78	13
P. clavipes (on wheatfeed)	25	♀	7	68	105
		♂♀	11	64	66
	22·5	♀	6	53	84
		♂♀	10	55	66
	20	♀	17	73	43
		♂♀	11	72	38
		♂♂	1	398	27
	17·5	♀	9	222	30
		♂♀	7	253	34
	15	♀	3	450	40
		♂	8	375	35
P. latro, auct. (on wheatfeed)	25	♀	21	71	159
	22·5	♀	14	64	78
	20	♀	1	78	63
		♀	17	363	48
	17·5	♀	26	314	47

In the present series of papers, larval diapause and a prolonged adult quiescence has been observed in *P. fur*, *P. pusillus*, *P. clavipes*, *P. latro*, auct., *P. villiger* and *P. sexpunctatus*. Linsley & MacSwain (1942) state that the adult of *P. californicus* remains quiescent in the cocoon throughout the winter and that all individuals in a single *Osmia* cell emerge simultaneously from their cocoons in February or March. The life-cycle of this American species and that of the European *P. sexpunctatus* appear to be very similar, but the emergence of adults is less concentrated in the European species. Emergence of adults of the latter species from a nest collected by Hamm (1924) extended over four months from November to February. Larval diapause is less clearly defined in *P. sexpunctatus* than in any other species studied. No diapause in the egg has been observed in any species, but one pupa of *P. villiger* produced an adult after a long delay. Smallman & Gray (1948) state that overwintering larvae of *P. villiger* may pupate in the spring but if they do, do not develop into adults until late summer, very little in advance of the normal emergence of adults. There may, therefore, be a facultative pupal diapause in the life-cycle of this species.

In Britain and Europe, adult spider beetles are most abundant in late September or October but many of the individuals present may live until early June. The majority of eggs of many species are probably laid in October and the spring. If a warm spring or summer accelerates development, then species such as *Ptinus tectus* or *Pseudeurostus hilleri* may become very abundant, and with others such as *Niptus hololeucus*, the adults may appear earlier than usual. In a very cool year the reverse effects result from retarded development. With species of *Ptinus* other than *P. tectus*, however, although a warm year accelerates development to the adult in the cocoon, the adult quiescent period increases and delays the emergence until autumn. If cool weather retards development slightly, then larval diapause may carry these individuals through the subsequent summer to the following autumn. It is possible for the life-cycle of *P. clavipes*, *P. fur* and *P. sexpunctatus* to be completed in just over four months in the temperature range 23–33°C. so that eggs laid in the spring may give rise to adults during the following autumn. At temperatures near 20°C. for most individuals the life-cycle is increased to 6–9 months, which enables eggs laid in the late autumn of one year to become adult early in the following autumn. At 22·5–27·5°C., *P. pusillus* also completes the life-cycle in 6–9 months. A yearly cycle is probable for *P. latro*, auct., at temperatures above 22·5°C. and for *P. pusillus* at 20°C. With temperatures below 20°C. for all these species and for some individuals of *P. fur* at 20°C. the cycle is further prolonged and may last from 15 months to two years. Whatever the length of developmental cycle, adults do not emerge before early September. Adults of *P. sexpunctatus* do not appear until November, and emergences continue until February with stragglers up to May (Hamm, 1924). This species and *P. californicus* presumably complete their feeding in one season as a rule since they depend on bees to provide their food and would have to rely on eating dead bees if the pollen and honey supply were depleted.

In all the species of *Ptinus* which have a diapause, the dormant period of the male adult is usually less than that of the female by at least ten days. Since there are no large sex differences in other developmental stages, it is clear that the first males emerge before the earliest females. These males probably wander, possibly flying, in search of females breeding elsewhere. Later emergences will include both sexes.

The introduction of a resting stage into a life-cycle, with the consequent restriction of the species to one generation a year at most, puts the species at a considerable disadvantage with related species that can multiply unhindered in suitable environmental conditions. This helps to explain the rapidity of the rise in the importance of *Ptinus tectus* after its introduction into Britain and its

replacement of *P. fur* as our most usual spider beetle. Since their introduction, *Niptus hololeucus* in some environments, as well as *Trigonogenius globulus* locally, also have both outnumbered native species of *Ptinus* although neither breeds very quickly at normal British temperatures and seldom completes more than one generation in a year. The recently introduced *Pseudeurostus hilleri* may be expected to increase in numbers and spread its range so long as it does not come into competition with *Ptinus tectus* (H.B. 13).

Resting stages are likely to be of advantage where the life of the species is tied to an annual cycle, as for instance for species living in nests, especially bees' nests, or for species with adults depending on certain flowers for pollen or nectar. Without a mechanism which ensures that adults or larvae are present when food is available, the species would depend entirely on the accident of having a life-cycle lasting approximately one year in existing environmental conditions or on being able to survive without food for long periods. The species included in the subgenus *Gynopterus*, which appear to be mainly dependent on bees, may be placed in this category.

A resting stage may also serve to help a species to survive during cold winters or possibly during hot or dry seasons. Adults of *Ptinus villiger*, which is the major spider-beetle pest in Canada (Smallman & Gray, 1948), emerge either in the autumn or in the spring. Both young adults and diapausing larvae can withstand temperatures down to −15°C. Another species of spider beetle which is frequently recorded from storage premises in cold areas is *P. raptor*. It can be confidently assumed that this species has resting stages which can survive the winter.

The remaining species of *Ptinus* presumably have invaded stores from nests but continue to exhibit a diapause no longer serving its original purpose. It may still be an asset, however, as these species are not common, and the restriction of adult emergence to a short period increases the chances of pairing and the growth of local colonies.

Adult Life.

All adult spider beetles are long-lived in satisfactory conditions, with the female usually living slightly longer than the male. Even at 25°C., which is a high enough temperature to shorten life considerably, the shortest mean life recorded by us has been 14 weeks for *P. fur*. In warehouses this species lives at least six months, and adults of *P. tectus* can live for two years. Most of the warehouse spider beetles live from 6 to 15 months in Britain.

All the adults of spider beetles drink from moist surfaces when able and react to a humidity gradient when they are desiccated. They are often trapped, therefore, in buckets of water, by damp rags and in wash-basins, and are attracted to fresh rat droppings and latrines. Denied access to fluid, the female lays few eggs, but if allowed to drink at will she lays many eggs at a fairly steady rate. The female of *P. tectus* can lay nearly a thousand eggs, *Mezium affine* nearly 500, *Gibbium psylloides* nearly 300. *Niptus hololeucus*, *Pseudeurostus hilleri*, *Tipnus unicolor*, *Trigonogenius globulus* and *Stethomezium squamosum* can all lay well over 100 eggs per female. Fewer eggs are laid by the females of those species which have a resting stage in the life-cycle. Nevertheless, individual females of *P. fur* can also exceed 100 eggs (Braune, 1943, p. 558). The figures available for *P. sexpunctatus* are very low, only 21 eggs per female. *P. latro*, auct. (Woodroffe, 1958*a*), reaches at least 40 eggs per female in culture. No figures are available for *P. clavipes* or *P. pusillus* but it seems probable from experience that they lay about 50 eggs per female. Mating is seldom observed and easily disturbed. It first occurs very soon after emergence from the cocoon and is repeated later at intervals. Females isolated after the first mating may,

after a time, lay only infertile eggs but will, if left undisturbed with a male for a few hours, regain the capacity of producing fertile eggs. Woodroffe (1958*a*) describes the mating of *P. latro*, auct. Spider beetles are negatively phototactic, and are most active in low light intensities. In bright light they search for a dark place and remain in it. Mating probably occurs mainly in the dark. Unmated females do not as a rule lay eggs in normal circumstances, but Woodroffe (1958*a*) found that exceptionally crowded populations of *P. latro*, auct., could be induced to lay many eggs. Two out of many thousand incubated eggs produced by unmated females of this species contained fully formed larvae. Mated females which for some reason are not producing viable eggs usually lay a subnormal number of eggs. These females produce viable eggs at a normal rate if impregnated again by a fertile male, and some start without obvious cause to produce numerous viable eggs after a period of laying a few infertile ones.

The Rate of Increase of Spider Beetles.

In the absence of a clear-cut lesion attributable to a pest species and where it is impossible to assess the weight losses it causes, the increase in numbers of the insect can be used as an index of damage. In some circumstances the potential damage can be estimated by predicting the increase in numbers, and the life-cycle data obtained in the laboratory may be used for this purpose (H. 8). The data required for this prediction (r) are the rate of development (R), the developmental (m) and adult mortality, the sex ratio (s) and the number of eggs laid, together with the oviposition pattern (E). Any environmental factor which influences any of these data affects the rate of increase of the species. The most important factors are temperature, humidity, food, population density and certain life-cycle and behaviour peculiarities. Effects on the rate of development have the most potent effect for rate of increase is affected directly by this factor whereas the effect of other factors is proportional to their logarithm: $r = R \log_e Es(1-m)$. No factor has been found which affects the sex ratio.

The effect of temperature.

Temperature is the most obvious factor influencing increase. The maximum temperature at which development is possible and the developmental optimum are both lower for spider beetles than for most storage beetles. Thus 25°C. is very close to the developmental maximum for *Niptus hololeucus* and *Tipnus unicolor*; 28°C. is close to the maximum of *Ptinus tectus* and probably is also for *Pseudeurostus hilleri*, *Trigonogenius globulus* and *Stethomezium squamosum*. For *Gibbium psylloides* and *Mezium affine* the maximum is higher, just above and just below 35°C., respectively. For *Ptinus pusillus* and *P. fur*, the maximum constant temperature for development is close to 30°C., but for *P. sexpunctatus* it is higher. *P. clavipes* can complete its life-cycle at 30°C. but this is probably near its limit as it probably is also for *P. latro*, auct. The optimum for rate of development is some 5°C. below the maximum for most of these species, but for *P. clavipes*, *P. latro*, auct., and possibly *P. fur* the optimum is about 22·5°C., seven degrees or more below the maximum. In those species of *Ptinus* which show a larval diapause or adult quiescence, the concept of an optimum for rate of development has little meaning, since the life-cycle is related to seasons, and the factors most affecting increase in these species are oviposition and mortality. The death-rate of growing larvae is usually low over a wide zone of temperature, from the developmental optimum downward, providing the humidity is at a favourable level, which for most spider beetles is between 50 and 90 per cent. R.H. Oviposition is reduced at temperatures above the developmental optimum although the maximum for oviposition is usually above the developmental maximum. Maximum egg-laying occurs at or just below the developmental

optimum, but at temperatures down to some 10°C. below this optimum the number of eggs laid is little affected although the rate of laying is progressively slowed and the laying period much increased. The oviposition rate generally reaches a peak in under three weeks and then declines slowly, but below 15°C. the peak is hardly noticeable. Development is possible down to about 15–20°C. below the optimum. For all stages the rate of development is reduced to about half by lowering the temperature from the optimum to a point about 8–10°C. below it. A further decrease of 5°C. again halves the developmental rate. The minimum threshold of development cannot be determined very precisely but may be below 5°C. for many warehouse spider beetles. Godan (1952) records the growth of *P. fur* on rape and poppyseed during six months in which the temperature did not exceed 8°C. Ewer & Ewer (1942) estimate 5–7°C. as the minimum for oviposition by *P. tectus*.

The temperature gradients experienced by spider beetles in warehouses are usually gentle, for these beetles are unlikely to occur in heating produce and are seldom subject to direct sunlight. Gunn & Walshe (1942), in the only good paper dealing with the temperature preferences of a spider beetle, show that *P. tectus* exhibits successful avoiding actions when approaching low temperatures in a gentle gradient but not in a steep one. These observations were made in a circular apparatus with a spacious floor. In an elongate apparatus, spider beetles can be expected to keep close to the wall with one side against it. When walking in such a position they appear reluctant to turn around. Consequently a form of trapping may occur when they approach the limits of their comfortable temperature range, for they may become inactive rather than turn around. Gunn & Walshe, when using an elongate apparatus, obtained a preferred zone at 3–5°C., which is above the immobilisation temperature, for active adults of *P. tectus* have been observed in warehouses at 0°C. They obtained another preferred zone at 22–24°C., which is below the point at which they introduced the experimental insects (26–27°C.). These preferred zones were obtained by totalling all their experimental results. Individual experiments varied considerably. In some, only one of the peaks of preference appeared. The position of the peaks varied up to 3°C. in each direction. They may well mark the approximate limits of the favourable zone for the species, rather than preference temperatures. Gunn & Walshe showed that if the temperature of the air surrounding adults of *P. tectus* was raised slowly, they started to move to cooler conditions at 30°C., all having left by the time 33°C. was reached.

Temperatures above the maximum for development are rapidly fatal to adult spider beetles. At 5°C. above the maximum, death follows in about a month; at 10°C. above the maximum, death occurs within a day. On the other hand, spider beetles are resistant to cold. None are killed by the British winter (Solomon & Adamson, 1955) and *P. villiger* survives where temperatures of −15°C. are reached (Smallman & Gray, 1948). *P. tectus* is eliminated by about 50 days at −5°C. (H.B. 9). In a warehouse environment, the temperature conditions are often fairly constant, but there may be marked seasonal or diurnal changes. As a result of diurnal changes, spider beetles may be exposed for a short period every day to extreme temperatures. The effect of these exposures is less severe than a continuous exposure, but it has been found (Howe, 1956*b*) that daily exposure to temperatures above the developmental maximum are fatal if the overall mean temperature is near or above this maximum even when a considerable period is spent at optimal or lower temperatures.

The effect of humidity.

Humidity has a marked effect on the rates of developmental mortality and oviposition, all being adversely affected by low humidity. Spider beetles cannot multiply at relative humidities below 40 per cent.

The effect of food.

Food influences may be due to nutritive values or to physical features which determine how easily it is obtained and used. The chief limiting factors in nutritive values appear to be vitamins, for most poor foodstuffs were improved by the addition of five per cent. of yeast powder, whereas growth on good foodstuffs was rarely speeded up by this addition. The diet must also contain a sterol. The relative proportions of protein and carbohydrate appear to be unimportant and a diet containing only 10 per cent. of protein is adequate. The best results are obtained when from a quarter to a half of the diet is protein. Too much fat in the food renders it physically unsatisfactory, as does too much sugar, which absorbs water and makes the food sticky. Other foodstuffs may be too hard for young larvae to penetrate or abrade, and these (*e.g.*, dried potato strips) are often excellent foodstuffs when ground into a meal. Even if the foodstuff is soft, the ability of the larva to "handle" it affects the rate of growth. Thus whole grains of a soft wheat are not so suitable a food as wholewheat flour because they are not so easily eaten. The particle size of homogeneous foodstuffs sometimes affects the rate of development (H. 2, H.B. 9), the finest foodstuffs being more satisfactory than the coarsest, probably due to the ease of utilising small particles. With more heterogeneous foods, such as whole flour and some samples of fishmeal, sieving produces samples of different nutritive values.

Wheatfeed, used as a standard food in this series, is about the best food for all warehouse spider beetles and is not improved by the addition of yeast. Dried insects are also a good foodstuff, and flour and other cereal derivatives are nearly as satisfactory. Fishmeal is inadequate for *Niptus hololeucus* and nearly related species, which presumably have additional vitamin requirements because this is a fairly good food for the remaining species. The length of the development cycle can be doubled through feeding on a poor food, and mortality may exceed 90 per cent.

Food may also affect oviposition. Texture and perhaps smell may determine whether the female lays eggs in the food. Nutritionally, the heavy adult produced from a well-fed larva may have a greater egg potential, and as the adult is long-lived, adult feeding may determine how many eggs are developed later in life. The heaviest adults are produced by the same foods that are classified as best on the criterion of fast growth. Larvae happening to eat others during growth produce heavy adults. Any factors slowing growth in the normal temperature range, such as poor food or low humidity as well as extreme temperatures, also reduce the size of the adult produced. The food value of materials to adult spider beetles is probably of little importance compared with the water supply, but a need for protein might be expected. It is interesting to note, therefore, that *Pseudeurostus hilleri*, which cannot as a larva develop on fishmeal, laid many more eggs in a culture medium of fishmeal than in wheatfeed, in which its larva thrives. It appears unlikely that spider beetles show much preference for one foodstuff as an oviposition site when a choice is available, although in a warehouse they seemed to prefer materials present in small quantity (H. 5), *i.e.*, they laid much better in baits put down in a warehouse if the bait material was different from that in store. In laboratory experiments there was little consistent preference for one kind of food as an oviposition medium (H.B. 7). *Stethomezium squamosum* and *Ptinus fur*, however, consistently preferred fishmeal to wheatfeed or flour; *Niptus hololeucus*, *Pseudeurostus hilleri* and *Ptinus sexpunctatus* laid few eggs in fishmeal and many in the cereal products; *Trigonogenius globulus*, whilst laying quite well in fishmeal, laid more in the cereal products. It is noteworthy that *Pseudeurostus hilleri* does not choose to oviposit in fishmeal but if given no choice lays very well in it (see above).

The effect of population density.

Gunn & Knight (1945) showed that the rate of development of larvae of *Ptinus tectus* was reduced if two larvae were grown together in the same tube even if the amount of food and space per larva was maintained. If space and food were kept constant and the number of larvae increased in laboratory experiments, the maximum effect on developmental rate (a reduction of nearly 15% each) was observed by an increase from 1 to 2 or 2 to 4 larvae per tube, further increases to 8 or 16 larvae per tube progressively reducing the growth rate by less than 10 per cent. each. Crowding also markedly reduced the weight of the beetles bred, although the available food supply was adequate for attaining normal size. Developmental mortality was increased and cannibalism introduced, for a feeding larva may break into a cocoon and eat the prepupa or pupa inside. Crowding also affects oviposition, mainly due to mutual interference and to a tendency for adults to collect into stationary groups, and probably also to the eating of eggs by both adults and larvae. Freshly hatched larvae in search of food will puncture eggs and eat the contents, so that in experimental work there is usually a poor percentage hatch of eggs if they are kept in large groups without food.

The effect of life-cycle peculiarities.

The chief feature of the life-cycle which affects the concept of rate of increase is the occurrence of the resting stages, which not only ensure that the generation length will be approximately one or two years but prevent the appearance of a stable age distribution. With species of spider beetles having a diapause, however, the average number of female beetles produced by a female is roughly the rate of increase per annum, though these offspring may appear partly in one autumn and partly in the next. The environmental conditions determine the proportion of larvae completing growth in one season. In these circumstances, the calculations performed in an earlier paper (H. 8) for *Ptinus fur* and *P. sexpunctatus* are inappropriate, but they may apply when populations of these species have been reared in cultures or in heated premises sufficiently long for the seasonal cycle to break down. The calculation for *P. sexpunctatus* (H. 8) illustrates how the introduction of diapause can be dealt with, but the major difficulty remaining is that the proportion of larvae entering diapause cannot be predicted.

There is a number of other factors which affect the rate of increase in an unpredictable manner, mainly by affecting oviposition. The number of hours of darkness during which eggs are laid influences the number of eggs laid, as does staling of food. Both in the laboratory and in the warehouse, more eggs are laid in a sample of foodstuff on the first night it is available than on the subsequent nights. Mechanical disturbance discourages both oviposition and larval growth. There is a suggestion that the age of the female at the time of oviposition may somehow influence the rate of development (H. 4). Ludwig (1956) has made a similar observation for *Tenebrio molitor* L. There is no information to show if interspecific competition among spider beetles is different in effect from intraspecific crowding. Several species are frequently found together, and if there is a tendency to mutual exclusion it must be a slow process, perhaps because the rate of increase is slow in most species.

A value for the rate of increase has been calculated for all the warehouse spider beetles which do not exhibit a diapause (H. 8; H. 12; H.B. 13). The order of magnitude of these values corresponds closely with the relative success of these species. If 20°C. is taken as the maximum average temperature experienced in British warehouses, then *Ptinus tectus* will increase at a maximum rate of 32 per cent. per week, *i.e.*, doubling in three weeks. At this temperature,

Pseudeurostus hilleri increases at most by 27 per cent. per week, *Niptus hololeucus* by 19 per cent. and *Tipnus unicolor* by 12 per cent. weekly, the latter being equivalent to doubling in seven weeks. Rough estimates for other species are *Trigonogenius globulus*, 17 per cent.; *Gibbium psylloides*, 13 per cent.; *Stethomezium squamosum*, 13 per cent.; and *Mezium affine*, 9 per cent. At 15°C., *Ptinus tectus* is still able to increase by 16 per cent. per week. Very approximate figures for the other species at this temperature are *Pseudeurostus hilleri*, 14 per cent.; *Tipnus unicolor*, 10 per cent.; *N. hololeucus* and *Trigonogenius globulus*, 9 per cent.; *S. squamosum*, 7 per cent.; *G. psylloides*, 6 per cent.; and *M. affine*, 4 per cent. In a warehouse (H. 8), *Ptinus tectus* was found to increase by 27 per cent. per week over a period of eight weeks in small bags of fresh wheatfeed, after which the rate of increase diminished because of crowding.

Predictions as to Spread of Warehouse Spider Beetles.

During the past century, several spider beetles have spread spectacularly around the world. The present series of papers has given some information on the environmental requirements of some species. From these data we may conclude that after *Ptinus tectus*, the most successful of the well established species, there will not be any further examples of worldwide spread unless some new species invades warehouses. The distribution of each species in warehouses is controlled by its temperature, humidity, food and water requirements, its ability to withstand temperature extremes and dryness, and the degree to which it may be carried around by trade. It is possible, but unlikely, that there are new areas open to trade which might introduce new spider beetles into commerce. In this work, enough data to draw theoretical distribution maps have been obtained only for *Ptinus tectus* (H.B. 9, fig. 19). Maps drawn for *Niptus hololeucus*, *Pseudeurostus hilleri*, *Stethomezium squamosum* and *Trigonogenius globulus* would be very similar; *Tipnus unicolor* is probably restricted to cooler regions while *Ptinus fur*, *P. pusillus*, *P. clavipes*, *P. latro*, auct., and *P. sexpunctatus* could live in warmer regions, the U.S.A. for instance. *Gibbium psylloides* and *Mezium affine* are probably restricted only by dryness.

In practice, insects, including spider beetles, are often imported into areas where they cannot survive even in the absence of control measures. Thus maps for the distribution of storage insects based on collecting records need to be augmented by statements as to whether the species is established, and if so whether in heated premises. The map given in the *Canadian Insect Pest Review* (vol. 34, facing p. 159, 1956) for *P. tectus* (cited as *P. ocellus* Brown), for instance, includes occurrence records for places where its establishment would be noteworthy outside heated premises.

Discussion.

One of the reasons for including many species of one family in this work was to make it possible to compare and contrast closely related forms and determine the factors which make some species important and others not. This has been summed up in the single figures which express the rate of increase. Another reason for studying a group is that it is possible to split them into sub-groups on biological characteristics. Thus the species exhibiting a clear-cut larval diapause form one group (*Ptinus fur*, *P. clavipes*, *P. pusillus*, *P. villiger*), and *P. sexpunctatus*, which has a less well defined larval diapause, is evidently close to this group. This latter species may be grouped with *P. californicus*, *P. exulans* and *P. vaulogeri* on the grounds that all are found in the nests of bees. Since *Gibbium psylloides* and *Mezium affine* have higher temperature optima than the rest, they form another group, and *Niptus hololeucus*, *Pseudeurostus hilleri* and *Tipnus unicolor*, which have lower temperature optima and have been found to

be unable to subsist on fishmeal, form another. The remaining species are *Stethomezium squamosum*, *Trigonogenius globulus* and *Ptinus tectus*. It is interesting to note how closely these biological groupings correspond to the taxonomic ones mentioned at the beginning of this paper. *Stethomezium squamosum*, which differs a little from other GIBBIINAE in larval structure and lacks their characteristic "blood globule" appearance, also differs slightly in temperature relations. Similarly *Ptinus tectus*, which is quite distinct both as adult and larva among storage species of *Ptinus*, is very different in biology. There appear to be strong reasons for placing *P. tectus* in at least a distinct subgenus.

The winged species of spider beetle are presumably the more primitive in this respect, and loss of wings a specialisation. The primitive species are found in association with bees and dead or dying wood. No fully winged species is known to breed in warehouses, although it is clear that *P. sexpunctatus* and *P. californicus* can breed in stored cereals. The species which have retained wings in the male have also retained the larval diapause and adult dormancy and hence tend to be seasonal in occurrence. There are some signs in laboratory cultures that in nearly constant conditions these resting stages are unable to maintain the seasonal rhythm. In *P. fur*, the adult dormancy is much shorter than in other seasonal species in warehouses.

Species which have lost the wings in both sexes, and *P. tectus* in which the wings are usually reduced, do not exhibit a diapause. In the sheltered life of warehouses these species are generally more successful than those species which do have a diapause. Loss of wings is no handicap to a storage species whereas the absence of a diapause removes a check to the rapid increase of the species. Diapause may be an adaptation to life in the nests of insects, birds or mammals in which some sort of seasonal cycle exists. In this type of habitat loss of wings might inhibit dispersal of the species. When a nest is used once only, both sexes must be winged, for the female must find a new nest in which to lay eggs. If the nest is reoccupied each year, the female can remain in the nest in which she developed, but if the population is not to inbreed, the males must be able to fly. Consequently it can be postulated that the diapausing species with winged males are primarily inhabitants of the nests of birds and bats which have invaded human storehouses. The species associated with the nests of bees have not invaded warehouses because the bees seldom nest in or near these buildings. The wingless species of spider beetle were probably introduced into storehouses by rats and other rodents. These animals quickly invaded human storage caches and built nests in which the amount of seasonal change may be small. The wingless spider beetles probably invaded birds' nests from warehouses, and seem to have had little difficulty in spreading to comparatively inaccessible nests in spite of the absence of wings.

In conclusion, it may be mentioned how little is known about such an interesting and compact group as the PTINIDAE, how little information there is to add to that obtained from the small number of storage forms. The adult taxonomy is poorly known, without adequate descriptions of genera or subgenera and with few descriptions of larvae. It is well known that some species feed on droppings, carrion and on the foodstores of other species, but the feeding habits of the many species associated with dead trees are not known, which is most remarkable in view of the close relationship of the family to the wood-boring ANOBIIDAE.

The significance of the absence of wings is not understood, and too little is known of the habits or habitats of winged and wingless species or of those winged only in the male. The wingless species of spider beetles are surprisingly mobile and at present we can only guess the ways in which they spread to warehouses, houses and nests. The forms which have retained normal wings in the female

have not become important in storage. We do not know if any of the outdoor species has a diapause or what advantage diapause might confer on them. Clearly, therefore, the taxonomy of the group needs further work, together with a biological study of some outdoor species.

Among the warehouse forms, a considerable amount of further work is needed to augment that presented here. All specimens collected must be accurately identified, and the environment recorded, together with observations showing whether or not the species is established. The spider beetles could form an interesting group to compare for food requirements, especially of vitamins or accessory substances. The ease of breeding would make this a useful group for use in biological experiments where very fast growth was not needed.

Summary.

The identification of spider beetles found in storage premises, especially of species of *Ptinus s.l.* and *Mezium* has frequently been incorrect. The inadequacy of the present descriptions of genera and subgenera of spider beetles is pointed out. Grouping of the storage species by adult and larval characters corresponds well. The recorded world distribution of species is shown in a Table.

Species of spider beetle considered to be native to Britain are *Ptinus lichenum* Marsham, *P. palliatus* Perris and *P. subpilosus* Sturm, which are not found in storage premises, and *P. fur* (L.), *P. sexpunctatus* Panz. and *Tipnus unicolor* (Pill. & Mitt.), which may be found in warehouses. Eight species and a gynogenetic form have been imported into Britain and have succeeded in becoming established, *Mezium affine* Boield., *Gibbium psylloides* (Czenp.) and *Niptus hololeucus* (Fald.), early in the nineteenth century, *Ptinus clavipes* Panz. and also its triploid form *mobilis* Moore (= *P. latro*, auct.) later in the nineteenth century, *Ptinus tectus* Boield., *Trigonogenius globulus* Sol. and *Ptinus pusillus* Sturm about the turn of the century, and finally *Pseudeurostus hilleri* (Rttr.) about 20 years ago. The status and distribution of each species is discussed. Only *Ptinus tectus* is a widespread pest in Britain.

The wide variety of food suitable for scavenging species which will utilise substances of both animal and vegetable origin is stressed. Spider beetles are especially attracted to moisture and excrement and as a result will occur in the protected nests of other species of animal. Published records of associations of spider beetles with nests are summarised in a Table. Animal droppings and dead insects enable spider beetles to grow rapidly. Wool, hair and feathers, textile fabrics, old wood and a number of apparently non-nutritive substances are damaged by spider beetle larvae which seem to be able to grow on some of these substances.

Damage caused by spider beetles is mainly indirect, contamination due to frass, silk and fragments of dead insects, the boring of holes in containers and spinning of cocoons on the containers. Actual loss of weight due to feeding is small unless the beetle population is enormous.

A large proportion of the adult spider-beetle population of a warehouse inhabits cracks in the floors or walls and spreads from there to the peripheral part of stacks of produce where eggs are laid, producing a superficial infestation. Adult spider beetles are chiefly active at night. Parasites and predators recorded as attacking spider beetles are listed, and methods of culturing species are described.

Spider beetles usually have three larval instars, but adverse conditions may increase their number. The total developmental period is long compared with other families of warehouse beetles. Most spider beetles have a normal life-cycle but some species of *Ptinus* have a facultative larval diapause and an adult dormant period preceding emergence from the cocoon. The diapause and

dormancy enable adults of these species to emerge in the autumn regardless of the weather during the previous season. Adults live from 6 to 15 months. At constant temperature, eggs are laid at a steady rate, the number being laid varying from under 50 in some species of *Ptinus* to nearly 1,000 in *P. tectus*.

The influences of temperature, humidity, food, population density and of diapause and dormancy on the rate of increase of spider-beetle species is discussed. The most rapid increase possible for these species in Britain is doubling in three weeks by *P. tectus*. It is concluded that *P. tectus* is unlikely to be superseded as the most important spider beetle of cool temperate areas and that, elsewhere, spider beetles will not attain the importance of this species.

Grouping the species on their biological features corresponds with the taxonomic relationships of the family.

Acknowledgements.

I should like to thank Dr. H. D. Burges and Miss J. E. Currie for invaluable help in carrying out the work described in this series of papers; Mr. L. P. Lefkovitch and Mr. G. E. Woodroffe for the information and ideas arising from discussions with them and to the staff of the libraries of this laboratory, the Commonwealth Institute of Entomology and the Royal Entomological Society of London. I am grateful to Prof. M. H. Hatch for pointing out our error concerning the first North American record of *P. tectus*.

This work has formed part of the programme of the Pest Infestation Laboratory of the Department of Scientific and Industrial Research.

References.

Arnhart, L. (1929). Der Räuber-Bohrkäfer (*Ptinus raptor*, Str.) ein Pollenzerstörer.—*Neue Bienenztg* **28** pp. 159–160.

Ashe, G. H. (1924). *Ptinus sexpunctatus* Panz. at Hartlebury.—*Ent. mon. Mag.* **60** p. 87.

Auten, M. (1925). Insects associated with spider nests.—*Ann. ent. Soc. Amer.* **18** pp. 240–250.

Azambre, A. (1855). [Habitudes naturelles du *Ptinus sex-pustulatus*.]—*Ann. Soc. ent. Fr.* (3) **3** pp. lii–liii.

Baeta Neves, C. M., Cancela da Fonseca, J. P. & Monteiro Guimarães, J. A. (1956). A entomofauna dos produtos armazenados em Portugal (Metrópole e Ultramar).—*Ann. Jta Miss. geogr.* **11** pp. 117–142.

Bainbridge, W. (1837). Notice of the recent occurrence in London of *Ptinus hololeucus* of Faldermann.—*Proc. ent. Soc. Lond.* **1** p. lxvii (Mtg of 6 Nov. 1837).

Bargagli, P. (1884). Note intorno alla biologia di alcuni coleotteri.—*Boll. Soc. ent. ital.* **16** pp. 92–96.

Bartels, L. (1915). [Title not known.]—*Neue Bienenztg* **14** (pages unknown). [Reference from Arnhart (1929).]

Bedel, L. (1872). [Note sur la manière de vivre du *Ptinus sexpunctatus*.]—*Bull. Soc. ent. Fr.* (5) **2** p. li.

Beirne, B. P. (1952). Insects found in foodstuffs and stored products in Ireland.—*Ent. Gaz.* **3** pp. 81–84.

Bentley, E. W. (1944). The biology and behaviour of *Ptinus tectus* Boie. (Coleoptera, Ptinidae), a pest of stored products. V. Humidity reactions.—*J. exp. Biol.* **20** pp. 152–158.

Bentley, E. W., Gunn, D. L. & Ewer, D. W. (1941). The biology and behaviour of *Ptinus tectus* Boie. (Coleoptera, Ptinidae), a pest of stored products. I. The daily rhythm of locomotory activity, especially in relation to light and temperature.—*J. exp. Biol.* **18** pp. 182–195.

Bickhardt, H. (1911). Verzeichnis der in den Nestern von Warmblütern gefundenen Käfer.—*Arch. Naturg.* **1** Suppl. pp. 11–18.

Blackwelder, R. E. (1945). Checklist of the Coleopterous insects of Mexico, Central America, the West Indies and South America. Part 3.—*Bull. U.S. nat. Mus.* no. 185 pp. 343–550.

Blair, K. G. (1924). *Ptinus sexpunctatus* Panz. in a bird's nest.—*Ent. mon. Mag.* **60** p. 117.

Blair, K. G. (1930). *Ptinus pusillus* Sturm in London.—*Ent. mon. Mag.* **66** p. 43.

Boieldieu, A. (1856). Monographie des Ptiniores.—*Ann. Soc. ent. Fr.* (3) **4** pp. 285–315.

Böving, A. G. (1956). A description of the mature larva of *Ptinus californicus* Pic and a discussion about the justification of considering the Ptinidae as a valid family of beetles.—*Ent. Medd.* **27** pp. 229–241.

Brassler, K. (1929). *Ptinus raptor* Str. als Schädling im Bienenstock.—*Z. angew. Ent.* **15** pp. 635–637.

Braune, R. (1943). Vergleichende Untersuchungen an den Diebskäfern *Ptinus tectus* Boield., *Ptinus fur* L., *Ptinus latro* Fabr., *Ptinus sexpunctatus* Panz., und *Ptinus brunneus* Duft., zugleich der experimentelle Beweis für die Notwendigkeit des Flüssigkeitsausgleichs im Insektenkörper.—*Z. Morph. Ökol. Tiere* **39** pp. 546–691.

Bridwell, J. C. (1919). Some notes on Hawaiian and other Bethylidae (Hymenoptera) with descriptions of new species.—*Proc. Hawaii. ent. Soc.* **4** pp. 21–38.

Brinck, P. (1945). Coleoptera.—*Sci. Res. Norweg. Antarctic Exped.* no. 24, 23 pp.

Briscoe, M. S. (1956). Kinds and distribution of wild rodents and their ectoparasites in Egypt.—*Amer. Midl. Nat.* **56** pp. 393–408.

Broun, T. (1914). Descriptions of new genera and species of Coleoptera. Part III.—*Bull. N.Z. Inst.* **1** pp. 143–266.

Brown, W. J. (1940). A key to the species of Ptinidae occurring in dwellings and warehouses in Canada (Coleoptera).—*Canad. Ent.* **72** pp. 115–122.

Brown, W. J. (1944). Some new and poorly known species of Coleoptera, II.—*Canad. Ent.* **76** pp. 4–10.

Butler, E. A. (1896). Ptini in a hornet's nest.—*Ent. mon. Mag.* **32** p. 109.

Caillol, H. (1908–14). Catalogue des Coléoptères de Provence **3** pp. 109–110.

Champion, G. C. (1913). *Codiosoma spadix*, Herbst, in New Zealand.—*Ent. mon. Mag.* **49** p. 32.

Chevalier, L. (1923). Étude sur la biologie et la manière de vivre de *Ptinus sexpunctatus* Panz., coléoptère mangeur de miel.—*Bull. Soc. Sci. Seine et Oise* (2) **4** pp. 30–32.

Chittenden, F. H. (1896). Insects affecting cereals and other dry vegetable foods.—*Bull. U.S. Bur. Ent.* (N.S.) no. 4 pp. 112–130.

Chitty, A. J. (1904). *Ptinus tectus* and *Lathridius bergrothi* in Holborn.—*Ent. mon. Mag.* **40** p. 109.

Cornelius, C. (1869). Vogelnester und Insecten.— *Ent. Ztg* **30** pp. 407–410.

Cotterell, G. S. (1952). The insects associated with export produce in southern Nigeria.—*Bull. ent. Res.* **43** pp. 145–152.

Cox, H. E. (1874). A handbook of the Coleoptera or beetles of Great Britain and Ireland.—2 vols. London.

Cros, A. (1932). *Ptinus vaulogeri*, étude biologique.—Livre centen. Soc. ent. Fr. pp. 345–351.

Crowson, R. A. (1955). The natural classification of the families of Coleoptera. —187 pp. London, Lloyd.

Curtis, J. (1824–39). British entomology. London. (1828) **5** no. 232; (1831) **8** no. 342; (1837) **14** no. 646.

Curtis, J. (1883). Farm insects.—528 pp. London, van Voorst.

Davis, A. C. (1934). Notes on the insect inhabitants of wood-rat houses in California.—*Bull. S. Calif. Acad. Sci.* **33** pp. 12–24.

Dobroscky, I. D. (1925). External parasites of birds and the fauna of birds' nests.—*Biol. Bull. Wood's Hole* **48** pp. 274–281.

Donisthorpe, H. (1906). *Ptinus pusillus* Stm., a species of Coleoptera new to Britain.—*Ent. Rec.* **18** p. 45.

Donisthorpe, H. (1927). The guests of British ants, their habits and life histories.—244 pp. London, Routledge.

Donisthorpe, H. (1931). An annotated list of the additions to the British Coleopterous fauna, made since the publication of the supplementary volume (VI) of Fowler's " Coleoptera of the British Isles ".—*Ent. mon. Mag.* **67** pp. 164–175.

Donisthorpe, H. (1941). *Ptinus hirtellus* Stm. (Col., Ptinidae), a British insect with notes on a few other species.—*Ent. mon. Mag.* **77** pp. 105–107.

Donisthorpe, H. (1947). Insects in a pigeon's nest.—*Ent. mon. Mag.* **83** p. 294.

Duffy, E. A. J. (1953). Lead cable severely damaged by *Ptinus tectus* Boieldieu (Coleoptera, Ptinidae).—*Bull. ent. Res.* **44** pp. 83–84.

Eichler, W. (1939). Gregarinen als Feinde von Vorratsschädlingen.—*Mitt. Ges. Vorratsschutz* **15** pp. 48–50.

van Emden, F. (1931). Zur Kenntnis der Morphologie und Oekologie des Brotkäfer-Parasiten *Cephalonomia quadridentata* Duchaussoy.—*Z. Morph. Oekol. Tiere* **23** pp. 425–574.

Enslin, E. (1925). Beiträge zur Kenntnis der Hymenopteren. IV.—*Dtsch. ent. Z.* **1925** pp. 177–210.

Escherich. K. (1914). Schädliche und nützliche Insekten in getrocknetem und verarbeitetem Tabak.—*Z. angew. Ent.* **1** pp. 260–265.

Essig, E. O. (1933). *Ptinus tectus* Boieldieu.—*J. econ. Ent.* **26** pp. 734–735.

Evans, J. W. (1943). Insect pests and their control.—178 pp. [Hobart] Dept. Agric. Tasmania.

Everts, E. (1921). Nieuwe vondsten voor de Nederlandsche Coleopterenfauna. XXXVII.—*Ent. Ber.* **6** pp. 21–26.

Ewer, D. W. & Ewer, R. F. (1942). The biology and behaviour of *Ptinus tectus* Boie. (Coleoptera, Ptinidae), a pest of stored products. III. The effect of temperature and humidity on oviposition, feeding and duration of life cycle.—*J. exp. Biol.* **18** pp. 290–305.

EWER, R. F. (1943). Diurnal activity of three insect pests of stored products.—*Nature, Lond.* **152** pp. 133–134.

FALCOZ, L. (1914). Contribution à l'étude de la faune des microcavernes. Faune des terriers et des nids.—*Ann. Soc. Linn. Lyon* **61** pp. 59–245.

FALL, H. C. (1905). Revision of the Ptinidae of boreal America.—*Trans. Amer. ent. Soc.* **31** pp. 97–296.

FAUVEL, A. (1883). Les espèces du genre Mezium Curtis.—*Rev. ent. Caen* **2** pp. 306–309.

FAUVEL, A. (1889). Liste des coléoptères communs à l'Europe et à l'Amérique du Nord [et premier supplement].—*Rev. ent., Caen* **8** pp. 92–174.

FOLLWELL, J. H. (1952). Notes on some Ptinidae of British Columbia (Coleoptera).—*Proc. ent. Soc. B.C.* **48** pp. 60–63.

FOWLER, W. W. (1890). The Coleoptera of the British Islands. Vol. IV.—London, Reeve.

FOWLER, W. W. & DONISTHORPE, H. (1913). The Coleoptera of the British Islands. Vol. 6 (supplement).—357 pp. London, Reeve.

FREEMAN, J. A. (1950). Methods of spread of stored products insects and origin of infestation in stored products.—*Proc. 8th int. Congr. Ent., Stockholm 1948* pp. 815–825.

FRIESE, H. (1923). Die europäischen Bienen (Apidae). 5. Lief.—pp. 401–456. Berlin & Leipzig, de Gruyter.

GEBIEN, H. (1939). Die Käfer des Niederelbgebietes und Schleswig-Holsteins. Ptinidae.—*Verh. Ver. naturw. Heimatforsch. Hamb.* **27** pp. 29–30.

GERHARD, K. (1909). Käfer in Nestern.—*Ent. Bl.* **5** pp. 128–132.

GIBSON, A. (1924). The occurrence of the Ptinid beetle, *Niptus hololeucus* Fald., in North America.—*Canad. Ent.* **56** pp. 74–76.

GIRARD, M. (1859). [Note sur le *Ptinus brunneus* trouvé dans les nids de pigeons.]—*Ann. Soc. ent. Fr.* (3) **7** p. cxx.

GODAN, D. (1952). *Ptinus fur* L. an Raps und Mohn.—*Z. hyg. Zool.* **40** pp. 289–296.

GUNN, D. L. & HOPF, H. S. (1942). The biology and behaviour of *Ptinus tectus* Boie. (Coleoptera, Ptinidae), a pest of stored products. II. The amount of locomotory activity in relation to experimental and to previous temperatures.—*J. exp. Biol.* **18** pp. 278–289.

GUNN, D. L. & KNIGHT, R. H. (1945). The biology and behaviour of *Ptinus tectus* Boie. (Coleoptera, Ptinidae), a pest of stored products. VI. Culture conditions.—*J. exp. Biol.* **21** pp. 132–143.

GUNN, D. L. & WALSHE, B. M. (1942). The biology and behaviour of *Ptinus tectus* Boie. (Coleoptera, Ptinidae), a pest of stored products. IV. Temperature preference.—*J. exp. Biol.* **19** pp. 133–140.

GÜNTHER, V. (1951). Remarques sur le sousgenre *Gynopterus* Muls. et Rey (Col., Ptinidae).—*Acta Soc. ent. Čsl.* **48** pp. 14–19.

HALL, D. W. & HOWE, R. W. (1953). A revised key to the larvae of the Ptinidae associated with stored products.—*Bull. ent. Res.* **44** pp. 85–96.

HAMM, A. H. (1924). *Ptinus scxpunctatus* Panz. bred from the cells of the bee *Osmia rufa* L. in Oxford.—*Ent. mon. Mag.* **60** pp. 29–31.

HARTLEY, J. C. (1957). [*Ptinus tectus* Boield. and *Niptus hololeucus* Fald. in tartaric acid.]—*Proc. R. ent. Soc. Lond.* (C) **22** p. 54.

Hartnack, H. (1943). Unbidden house guests.—Tacoma, Wash., Hartnack Publ. Co.

Hatch, M. H. (1933). *Ptinus tectus* Boieldieu in America.—*Bull. Brooklyn ent. Soc.* **28** pp. 200–202.

Hatch, M. H. (1943). *Ptinus tectus* damaging furs in Alaska.—*J. econ. Ent.* **36** p. 353.

Hatch, M. H. (1953). The beetles of the Pacific Northwest. Part 1. Introduction and Adephaga.—University of Washington Press, Seattle, pp. 25–29.

Hellén, W. (1925). Übersicht der Ptiniden (Col.) Finlands.—*Notul. Ent., Helsingf.* **5** pp. 118–123.

Herold, W. (1933). Über einige Wohnungsschädlinge (*Glyciphagus, Lathridius, Ptinus, Tenebrio*, und *Lariophagus*).—*Mitt. Ges. Vorratsschutz* **9** pp. 51–56.

Heselhaus, F. (1914). Über Arthropoden in Nestern.—*Tijdschr. Ent.* **57** pp. 62–88.

Heselhaus, F. (1915). Weitere Beiträge zur Kenntnis der Nidicolen.—*Tijdschr. Ent.* **58** pp. 251–274.

Hickin, N. E. (1941). Notes on mites found associated with cultures of Ptinid beetles.—*Ent. mon. Mag.* **77** p. 197.

Hickin, N. E. (1946). An association of the brown house-moth (*Hofmannophila pseudospretella* Staint.) with *Ptinus tectus* Boield. (Col.) and various species of mites.—*Ent. mon. Mag.* **82** p. 273.

Hicks, E. A. (1959). Check-list and bibliography on the occurrence of insects in birds' nests.—681 pp. Ames, Iowa St. Coll. Pr.

Hinton, H. E. (1941). The Ptinidae of economic importance.—*Bull. ent. Res.* **31** pp. 331–381.

Hinton, H. E. (1943*a*). *Stethomezium squamosum* gen. et. sp. n. infesting stored food in Britain, with notes on a South African Ptinid not previously recorded in stored products (Coleoptera).—*Proc. R. ent. Soc. Lond.* (B) **12** pp. 50–54.

Hinton, H. E. (1943*b*). House moths feeding on dead insects in or near spider webs.—*Entomologist* **76** pp. 4–5.

Hinton, H. E. & Greenslade, R. M. (1943). Observations on species of Lepidoptera infesting stored products. XI. Notes on some moths found in bird guano.—*Entomologist* **76** pp. 182–184.

Hirose, K. (1936). Insect pests of insect specimens and control methods. 2. [*In Japanese.*]—*Insect World* **40** pp. 281–283. (*Rev. appl. Ent.* (A) **24** p. 790.)

[Hopping, G. R.] (1937). Insects (or near relatives) of economic importance recently noted in British Columbia.—*Proc. ent. Soc. B.C.* **33** pp. 46–47.

Howe, R. W. (1940). New records of insects in grain stores.—*Ent. mon. Mag.* **76** pp. 73–75.

Howe, R. W. (1943). Life history data for *Ptinus tectus* Boie. (Coleoptera, Ptinidae) at 70% relative humidity at 21°C. and 25°C.—*Proc. R. ent. Soc. Lond.* (A) **18** pp. 63–65.

Howe, R. W. (1949). Studies on beetles of the family Ptinidae. 2. Fineness of foodstuffs as a factor influencing the rate of development of *Ptinus tectus* Boield.—*Ent. mon. Mag.* **85** pp. 189–190.

HOWE, R. W. (1950*a*). Studies on beetles of the family Ptinidae. III. A two-year study of the distribution and abundance of *Ptinus tectus* Boield. in a warehouse.—*Bull. ent. Res.* **41** pp. 371–394.

HOWE, R. W. (1950*b*). Studies on beetles of the family Ptinidae. 4. A note on an anomalous effect of parental age on the speed of development.—*Ent. mon. Mag.* **86** pp. 325–326.

HOWE, R. W. (1951). Studies on beetles of the family Ptinidae. V. The oviposition rate of *Ptinus tectus* Boield. under natural conditions.—*Bull. ent. Res.* **42** pp. 445–453.

HOWE, R. W. (1952). Entomological problems of food storage in northern Nigeria.—*Bull. ent. Res.* **43** pp. 111–144.

HOWE, R. W. (1953). Studies on beetles of the family Ptinidae. VIII. The intrinsic rate of increase of some Ptinid beetles.—*Ann. appl. Biol.* **40** pp. 121–133.

HOWE, R. W. (1955). Studies on beetles of the family Ptinidae. 12. The biology of *Tipnus unicolor* Pill. & Mitt.—*Ent. mon. Mag.* **91** pp. 253–257.

HOWE, R. W. (1956*a*). Studies on beetles of the family Ptinidae. 14. The biology of *Ptinus pusillus* Sturm.—*Ent. mon. Mag.* **92** pp. 331–333.

HOWE, R. W. (1956*b*). A method for obtaining a controlled daily temperature cycle.—*Ann. appl. Biol.* **44** pp. 188–194.

HOWE, R. W. (1957). Studies on beetles of the family Ptinidae. 15. The biology of *Ptinus hirtellus* Sturm and some notes on *P. latro* F.—*Ent. mon. Mag.* **92** pp. 369–372.

HOWE, R. W. (1958). Studies on beetles of the family Ptinidae. 16. The developmental period of *Ptinus clavipes* Panz. form *mobilis* Moore (=*P. latro* auct.).—*Ent. mon. Mag.* **94** pp. 236–237.

HOWE, R. W. & BULL, J. O. (1956). Studies on beetles of the family Ptinidae. 13. The oviposition rate of *Pseudeurostus hilleri* (Reitt.).—*Ent. mon. Mag.* **92** pp. 113–115.

HOWE, R. W. & BURGES, H. D. (1951). Studies on beetles of the family Ptinidae. VI. The biology of *Ptinus fur* (L.) and *P. sexpunctatus* Panzer.—*Bull. ent. Res.* **42** pp. 449–511.

HOWE, R. W. & BURGES, H. D. (1952). Studies on beetles of the family Ptinidae. VII. The biology of five Ptinid species found in stored products.—*Bull. ent. Res.* **43** pp. 153–186.

HOWE, R. W. & BURGES, H. D. (1953*a*). Studies on beetles of the family Ptinidae. IX. A laboratory study of the biology of *Ptinus tectus* Boield.—*Bull. ent. Res.* **44** pp. 461–516.

HOWE, R. W. & BURGES, H. D. (1953*b*). Studies on beetles of the family Ptinidae. 10. The biology of *Mezium affine* Boieldieu.—*Ent. mon. Mag.* **89** pp. 217–220.

HOWE, R. W. & BURGES, H. D. (1955). Studies on beetles of the family Ptinidae. 11. Some notes on *Ptinus villiger* Reit.—*Ent. mon. Mag.* **91** pp. 73–75.

HUBBARD, H. G. (1886). [Habits of *Mezium.*]—*Proc. ent. Soc. Wash.* **1** p. 14.

HÜSING, J. O. (1935). Ueber einen neuen Parasiten *Lariophagus distinguendus* Först. (Hym. Chalc.) an *Ptinus fur* L. (Col. Ptin.).—*Zool. Anz.* **110** pp. 324–326.

Jansson, A. (1919). Die Arthropodenfauna der Eichhörnchen Nester.—*Ent. Tidskr.* **40** pp. 75–92.

Jeannel, R. (1909). Biospeologica. X. Coléoptères (seconde série).—*Arch. Zool. exp. gén.* (5) **1** pp. 447–532.

Kalshoven, L. G. E. (1938). Invloed van insecten op de kwaliteit en verhandelbaarheid van indische landbouwproducten.—*Korte Meded. Inst. PlZiekt. Buitenz.* no. 24, 48 pp.

Kashef, A. (1956). Étude biologique de *Stegobium paniceum* L. (Col. Anobiidae) et de son parasite: *Lariophagus distinguendus* Först. (Hym. Pteromalidae).—*Ann. Soc. ent. Fr.* **124** pp. 5–88.

Kemper, H. (1938). Hausschädlinge als Bewohner von Vogelnestern.—*Z. hyg. Zool.* **30** pp. 227–236, 269–274, 291–297.

Kemper, H. (1939). Die Nahrungs- und Genussmittelschädlinge und ihre Bekämpfung.—*Hyg. Zool.* **6,** 270 pp. Leipzig, P. Schops.

Kemper, H. (1951). Beobachtungen an *Cratacrina pallida* Latr. und *Melophagus ovinus* L. (Diptera, Pupipara). I. Beitrag.—*Z. hyg. Zool.* **39** pp. 225–259.

Kemper, H. (1956). Befall einer Kerze durch Diebskäfer.—*Anz. Schädlingsk.* **29** pp. 57–58.

Kiritani, K. (1957). The investigations on the faunal compositions in stored products. II. The faunal composition in relation to kinds of stored products. [*In Japanese with English summary.*]—*Jap. J. appl. Ent. Zool.* **1** pp. 8–14.

Kolbe, H. J. (1889). Einwanderung und Verbreitung des *Niptus hololeucus* Fald. in Europa.—*Ent. Nachr.* **15** pp. 3–7.

Koltze, W. (1901). Verzeichniss der in der Umgegend von Hamburg gefundenen Käfer.—*Verh. Ver. naturw. Unterh. Hamb.* **11** pp. 1–194.

Lea, A. M. (1905). On *Nepharis* and other ants' nest beetles taken by Mr. J. C. Goudie at Birchip.—*Proc. roy. Soc. Vict.* (N.S.) **17** pp. 371–385.

Lea, A. M. (1910). Australian and Tasmanian Coleoptera inhabiting or resorting to the nests of ants, bees, and termites.—*Proc. roy. Soc. Vict.* (N.S.) **23** pp. 116–230.

Lehnert, W. (1933). Beobachtungen über die Biocönose der Vogelnester.—*Orn. Mber.* **41** pp. 161–166.

Leleup, N. (1947). Contribution à l'étude des arthropodes nidicoles et microcavernicoles de Belgique.—*Bull. Ann. Soc. ent. Belg.* **83** pp. 304–343.

von Lengerken, H. (1924). Coleoptera I.—*Biol. Tiere Dtschl.* Lief. 10. Teil 40, pp. 1–36.

Leonardi, G. (1926). Elenco delle specie di insetti dannosi e loro parassiti ricordati in Italia fino all' anno 1911. Parte II, fasc. III.—*Ann. R. Ist. sup. agr. Portici* (3) **1** pp. 148–295.

Lepesme, P. (1945). Les coléoptères des denreés alimentaires et des produits industriels entreposés.—*Encycl. ent.* (A) **22,** 335 pp. Paris, Lechevalier.

Leruth, R. (1935). Exploration biologique des cavernes de la Belgique et du Limbourg hollandais. XXIVe contribution: Coléoptères.—*Bull. Ann. Soc. ent. Belg.* **75** pp. 201–285.

Linsley, E. G. (1942). Insect food caches as reservoirs and original sources of some stored products pests.—*J. econ. Ent.* **35** pp. 434–439.

Linsley, E. G. (1944). Natural sources, habitats, and reservoirs of insects associated with stored food products.—*Hilgardia* **16** pp. 187–224.

Linsley, E. G. & MacSwain, J. W. (1942). The bionomics of *Ptinus californicus*, a depredator in the nests of bees.—*Bull. S. Calif. Acad. Sci.* **40** pp. 126–137.

Linsley, E. G. & Michelbacher, A. E. (1943). A report on insect infestation of stored grain in California.—*J. econ. Ent.* **36** pp. 829–831.

Livingstone, E. M. & Reed, W. D. (1936). Insect fauna of cured tobacco in storage in the United States.—*J. econ. Ent.* **29** pp. 1017–1022.

Lloyd, R. W. (1945). Inhabitants of the jackdaw's nest.—*Ent. mon. Mag.* **81** p. 249.

Löw, F. (1867). Zoologische Notizen. Zweite Serie.—*Verh. zool.-bot. Ges. Wien* **17** pp. 745–752.

Ludwig, D. (1956). Effects of temperature and parental age on the life cycle of the mealworm, *Tenebrio molitor* Linnaeus (Coleoptera, Tenebrionidae).—*Ann. ent. Soc. Amer.* **49** pp. 12–15.

McAtee, W. L. (1929). Further notes on insect inhabitants of bird houses.—*Proc. ent. Soc. Wash.* **31** pp. 105–111.

Mallis, A. (1945). Handbook of pest control. The behaviour, life history, and control of household pests.—554 pp. [New York] MacNair-Dorland.

Maneval, H. (1929). Quelques précisions sur le mode de vie de *Ptinus sexpunctatus* Panz.—*Misc. ent.* **31** pp. 86–87.

Manton, S. M. (1945). The larvae of the Ptinidae associated with stored products.—*Bull. ent. Res.* **35** pp. 341–365.

Maréchal, P. (1929). Remarques sur la faune belge. Liste d'insectes intéressants, la plupart capturés en 1928.—*Lambillionea* **29** pp. 28–29.

Maréchal, P. (1932). Recherches sur deux Osmies communes: *O. cornuta* Latr. et *O. rufa* L. (Hymenoptera Apidae).—Livre centen. Soc. ent. Fr. pp. 505–512.

Maréchal, P. (1933). Sur quelques habitants des chaumes des toitures *Eriades maxillosus* L. (Hym. Apidae) et ses parasites, principalement *Trichodes alvearius* F. (Col. Cleridae).—*Bull. Ann. Soc. ent. Belg.* **73** pp. 227–258.

Mathur, R. N. (1956). Immature stages of Indian Coleoptera. (27). *Gibbium psylloides* Czempinski (family Ptinidae).—*Indian For. Rec.* (N.S.) Ent. **9** pp. 123–125.

Meeuse, A. D. J. (1952). On the origin of clothes moths, carpet beetles and similar household pests.—*Beaufortia* no. 15, 8 pp.

Moore, B. P. (1957). The identity of *Ptinus latro* auct. (Coleoptera, Ptinidae).—*Proc. R. ent. Soc. Lond.* (B) **26** pp. 199–202.

Moore, B. P., Woodroffe, G. E. & Sanderson, A. R. (1956). Polymorphism and parthenogenesis in a Ptinid beetle.—*Nature, Lond.* **177** pp. 847–848.

Morley, C. (1919). *Ptinus sexpunctatus* Panz. and *Osmia rufa* Linn.—*Ent. mon. Mag.* **55** p. 107.

Morris, H. M. (1937). Injurious insects of Cyprus.—*Bull. agric. Dep. Cyprus* no. 4 (Ent. Ser.) 31 pp.

Munster, T. (1933). Norske Ptinidae og Anobiidae.—*Norsk ent. Tidsskr.* **3** pp. 155–162.

Nicolas (—). (1892–93). *Ptinus sexpunctatus*.—*Échange* **8** pp. 143–145; **9** pp. 8–11.

Nielsen, E. T. (1932). Sur les habitudes des hyménoptères aculéates solitaires. I. (Bethylidae, Scoliidae, Cleptidae, Psammocharidae.)—*Ent. Medd.* **18** pp. 1–57.

Nordberg, S. (1936). Biologisch-ökologische Untersuchungen über die Vogelnidicolen.—*Acta zool. fenn.* **21,** 168 pp.

Obraztsov, N. S. (1928). On the distribution and biology of *Gibbium boieldieui* Levr. [*In Russian.*]—*Rev. russe Ent.* **22** pp. 134–136.

O'Farrell, A. F. & Butler, P. M. (1948). Insects and mites associated with the storage and manufacture of foodstuffs in Northern Ireland.—*Econ. Proc. R. Dublin Soc.* **3** pp. 343–407.

O'Mahony, E. (1939). Birds' nest beetles.—*Irish Nat. J.* **7** pp. 213–214.

Pax, F. & Maschke, K. (1935). Die Höhlenfauna des Glatzer Schneeberges. I. Die rezente Metazoenfauna.—Beitr. Biol. Glatzer Schneeberges **1** pp. 4–72.

Pence, R. J. (1955). Is new home construction upping the invasion of "strangers"?—*Pest Control* **23** no. 10 pp. 30, 32, 38, 40.

Pergande, T. (1886). [Breeding of *Ptinus brunneus.*]—*Proc. ent. Soc. Wash.* **1** p. 14.

Pescop, A. (1953). Spider beetles may mean rats.—*Pest Control* **21** no. 12 pp. 26, 37.

Pic, M. (1932). Les ptinides de France.—Livre centen. Soc. ent. Fr. pp. 513–516.

Picard, F. (1919). La faune entomologique du figuier.—*Ann. Serv. Epiphyt.* **6** pp. 34–174.

Pilate, G. R. (1905). Note on the finding of *Ptinus fur* and *brunneus*.—*Ent. News* **16** p. 80.

Pool, C. J. C. (1915). *Ptinus testaceus* Boieldieu; an old error corrected.—*Ent. mon. Mag.* **51** p. 328.

Rayment, T. (1935). A cluster of bees.—752 pp. Sydney, Endeavour Press.

Redtenbacher, L. (1874). Fauna Austriaca. Die Käfer. Band 2.—3rd edn. Vienna, Gerold.

Reh, L. (1929). Vom Messingkäfer.—*Mitt. Ges. Vorratsschutz* **5** pp. 39–40.

Reitter, E. (1911). Fauna Germanica. Die Käfer des Deutschen Reiches. Band 3.—436 pp. Stuttgart, Lutz.

Resch, F. (1874). Bewohner von Schwalbennestern.—*Natur u. Offenbar.* **20** p. 236.

Runner, G. A. (1919). The tobacco beetle: an important pest in tobacco products.—*Bull. U.S. Dep. Agric.* no. 737, 77 pp.

Rye, E. C. (1866). British beetles: an introduction to the study of our indigenous Coleoptera.—280 pp. London.

Rye, E. C. (1873). Coleoptera. New British species, corrections of nomenclature, etc., noticed since the publication of the Entomologist's Annual, 1872.—*Ent. Ann.* **1873** pp. 1–33.

Salmond, K. F. (1956). The insect and mite fauna of a Scottish flour mill.—*Bull. ent. Res.* **47** pp. 621–630.

Schaeffer, C. (1931). On a few new and known Coleoptera.—*Bull. Brooklyn ent. Soc.* **26** pp. 174–176.

Schmitt, C. (1929). Der Diebskäfer als Schmarotzer?—*Kosmos, Stuttgart* **26** pp. 72–73. [Reference from Linsley (1944).]

Schwarz, E. A. (1889). A new herbarium pest.—*Proc. ent. Soc. Wash.* **1** pp. 174–175.

Scott, H. (1921). The Ptinid beetle, *Trigonogenius globulum*, Solier, breeding in argol.—*Bull. ent. Res.* **12** pp. 133–134.

Shapiro, L. D. (1948). Ptinids and Dermestids destructive to wood. [*In Russian.*]—*Ent. Obozr.* **30** pp. 53–59.

Sharp, D. (1873). Note on *Tribolium confusum*, Duv., and *Ptinus testaceus*, Ol.—*Ent. mon. Mag.* **9** p. 268.

Smallman, B. N. & Gray, H. E. (1948). The control of spider beetles in eastern Canada. Warehouse pests.—10 pp. [? Ottawa] Canad. nat. Millers' Ass.

Solomon, M. E. & Adamson, B. E. (1955). The powers of survival of storage and domestic pests under winter conditions in Britain.—*Bull. ent. Res.* **46** pp. 311–355.

Spencer, G. J. (1942). Insects and other arthropods in buildings in British Columbia.—*Proc. ent. Soc. B.C.* **39** pp. 23–29.

Spittle, R. J. (1949). The coleopterous fauna of owls' nests.—*Ent. mon. Mag.* **85** pp. 78–79.

Stephens, J. F. (1829). A systematic catalogue of British insects.—London.

Stephens, J. F. (1839). A manual of British Coleoptera or beetles.—443 pp. London.

Székessy, V. (1948). Beitrag zur Kenntnis der Fauna einiger Vogelnester.—*Fragm. faun. Hung.* **11** pp. 62–64.

Székessy, V. (1950). Die Coleopteren-Fauna der Storchnester.—*Proc. 8th int. Congr. Ent., Stockholm 1948* pp. 497–507.

Tenhet, J. N. & Bare, C. O. (1951). Control of insects in stored and manufactured tobacco.—*Circ. U.S. Dep. Agric.* no. 869, 32 pp.

Tomlin, B. (1900). *Trigonogenius globulum*, Sol. in Lancashire.—*Ent. mon. Mag.* **36** p. 64.

Tuck, W. H. (1896). Inquiline and other inhabitants in nests of aculeate Hymenoptera.—*Ent. mon. Mag.* **32** pp. 153–155.

Tuck, W. H. (1897). Coleoptera, &c., in the nests of aculeate Hymenoptera.—*Ent. mon. Mag.* **33** pp. 58–60.

Ustinov, A. A. (1932). A review of pests in tobacco in Abkhazia observed in 1931. [*In Russian.*]—38 pp. Sukhum, Abkhaz. tabach. zonal'n. Sta.

Vappula, N. A. (1937). *Trigonogenius globulus* Sol. in Finnland angetroffen.—*Mitt. Ges. Vorratsschutz* **13** pp. 10–11.

Vogel, R. (1929). Zur Naturgeschichte des Messingkäfers (*Niptus hololeucus* Falderm.).—*Mitt. Ges. Vorratsschutz* **5** pp. 41–44.

Waddington, C. H. (1942). The development of rudimentary wings in *Ptinus tectus* Boield. (Coleoptera: family Ptinidae).—*Proc. zool. Soc. Lond.* (A) **112–113** pp. 13–20.

Wakefield, C. M. (1874). Notes upon certain recently-described new genera and species of Coleoptera, from Canterbury, New Zealand.—*Trans. Proc. N.Z. Inst.* **6** pp. 155–157.

Walker, J. J. (1920*a*). Coleoptera in the Oxford district during 1919.—*Ent. mon. Mag.* **56** pp. 14–15.

WALKER, J. J. (1920*b*). *Coninomus constrictus* Gyll. and other Coleoptera with *Acanthomyops* (*Lasius*) *fuliginosus* Latr.—*Ent. mon. Mag.* **56** pp. 209–210.

WEIDNER, H. (1952). Die Insekten der "Kulturwüste".—*Mitt. hamburg. zool. Mus.* **51** pp. 89–173.

WILSON, H. F. (1915). Insect pests of stored products.—*Bienn. Rep. Orc. agric. Exp. Sta. 1913–14* pp. 127–130.

WISE, K. A. J. (1956). Pests of stored products in New Zealand. II. Family Ptinidae (Coleoptera).—*N.Z. J. Sci. Tech.* **37B** pp. 503–508.

WOLLASTON, T. V. (1862). On the Ptinidae of the Canary Islands.—*Trans. ent. Soc. Lond.* (3) **1** pp. 190–214.

WOODROFFE, G. E. (1953). An ecological study of the insects and mites in the nests of certain birds in Britain.—*Bull. ent. Res.* **44** pp. 739–772.

WOODROFFE, G. E. (1954). An additional note on the fauna of birds' nests in Britain.—*Bull. ent. Res.* **45** pp. 135–136.

WOODROFFE, G. E. (1956). Some insects and mites associated with bat-roosts, with a discussion of the feeding habits of the cheyletids (Acarina).—*Ent. mon. Mag.* **92** pp. 138–141.

WOODROFFE, G. E. (1958*a*). The mode of reproduction of *Ptinus clavipes* Panzer form *mobilis* Moore (= *P. latro* auct.) (Coleoptera: Ptinidae).—*Proc. R. ent. Soc. Lond.* (A) **33** pp. 25–30.

WOODROFFE, G. E. (1958*b*). Birds' nests as a source of domestic insect pests.—*Ann. appl. Biol.* **46** p. 105.

WOODROFFE, G. E. & SOUTHGATE, B. J. (1951). Birds' nests as a source of domestic pests.—*Proc. zool. Soc. Lond.* **121** pp. 55–62.

XAMBEU, V. (1894). Moeurs et métamorphoses des insectes, 4e mémoire.— *Ann. Soc. ent. Fr.* **63** pp. 459–504.

XAMBEU, V. (1898). Moeurs et métamorphoses des insectes, 9e mémoire.—*Rev. Ent., Caen* **17** pp. 1–63.

YAKOBSON, G. G. (1913). Beetles of Russia and western Europe. A key for the determination of beetles. [*In Russian.*]—St. Petersburg.

ZACHER, F. (1928). Weitere Mitteilungen zur Biologie von *Niptus hololeucus*.—*Zool. Anz.* **79** pp. 269–272.

ZACHER, F. (1933). Haltung und Züchtung von Vorratsschädlingen.—*In* Abderhalden. *Handb. biol. Arb. Meth.*, Abt. IX. Teil 7 (Lief. 416) pp. 389–592.

ZACHER, F. (1938). Die Gliedertiere (Arthropoda) der Mühlen und Getreidespeicher in Deutschland.—*Mitt. Ges. Vorratsschutz, Sonderheft VII int. Kongr. Ent., Berlin 1938*, 48 pp.

ZACHER, F. (1939). Verschleppung und Einbürgerung von Vorratsschädlingen.—*Verh. 7. int. Kongr. Ent., Berlin 1938* **4** pp. 2919–2926.

ZACHER, F. (1948). Mitteilungen über Diebkäfer (Ptinidae) von wirtschaftlicher Bedeutung.—*Anz. Schädlingsk.* **21** pp. 97–103.

ZACHER, F. (1954). Die Einschleppung von Vorratsschädlingen in Deutschland.—*Verh. dtsch. Ges. angew. Ent.* **12** pp. 50–55.

ZIMMERMAN, E. C. (1940). On the genera of Anobiidae and Ptinidae found in Hawaii (Coleoptera).—*Proc. Hawaii. ent. Soc.* **10** pp. 467–470.

THE DEPOSITION OF AIRBORNE DROPLETS ON DEAD HOUSE-FLIES (*MUSCA DOMESTICA* L.).

By R. T. Jarman *

Chesterford Park Research Station, nr. Saffron Walden, Essex.

To make the best use of insecticidal liquids, they should be dispersed as droplets of the optimum size, and this varies according to the insect that is to be controlled and its habitat. Thus, to obtain contact kills on insects in flight within woodland, it is desirable that as little as possible of the chemical should be deposited wastefully on the vegetation. Large droplets, which are deposited readily on all surfaces, are soon filtered out. Green & Lane (1957) consider droplets less than 30μ dia. are necessary to penetrate vegetation, since these tend to be carried around the vegetation by the wind. However, very small droplets tend to be carried around the insects that are to be controlled. Thus, Latta & others (1947), La Mer & Hochberg (1949) and others, found that when DDT was dispersed as droplets with diameters progressively diminishing in size below 10μ, the dosage (concentration $\times$ time) of DDT needed to kill mosquitos by direct contact increased rapidly.

A. B. Hadaway and F. Barlow (unpublished results) carried out laboratory studies of the relative efficiency with which droplets of differing sizes were deposited on dead insects in possible resting sites, to obtain a fuller understanding of the processes occurring. They used a spinning-top sprayer (May, 1949) to produce uniform droplets in a wind tunnel, and placed insects on various discs and cylinders that were intended to simulate vegetation. They found that droplets having a diameter of 10μ tended to "flow" around both insect and "vegetation", those of 20μ were deposited on insects but not on "branches", while those of 60μ were deposited on both insects and "vegetation", and would therefore be filtered out by the latter. This work has been continued by measuring the efficiency with which droplets are deposited on dead insects in flying posture; house-flies (*Musca domestica* L.) were used as the test insects, and a cascade impactor (May, 1945) was used to find the concentration of the cloud of droplets.

Theory.

Droplets carried along in an air stream impact on objects in the airflow in varying proportions depending on the wind speed, the mass of each droplet, and the size and shape of the object. The processes that may be involved include inertia, interception and sedimentation. A droplet carried along by an air stream and approaching an obstruction tends to be diverted, following the stream, but its inertia may cause it to strike the object. In the case of interception, the trajectory of the circumference of a droplet may intersect the collecting surface, even if that of its centre does not do so. Sedimentation is the term given to the process whereby a droplet falling under gravity at an angle to the air stream consequently strikes the object.

Some particles do not stick firmly to the surface after hitting it; they may bounce off or be blown off by the air stream. Thus the degree of adhesion of the particle to the surface also affects the efficiency with which droplets are deposited.

We have considered the matter quantitatively by introducing the term

* Formerly of the Colonial Insecticides Research Unit, Porton, Wilts.

" collection efficiency " (E), defined as the quantity of a liquid deposited on the object, expressed as a percentage of the volume of liquid that would have passed through the same cross-sectional area as that of the object had the latter not been present.

Expressed mathematically we have,

$$E = \frac{100\,Q}{A\,U\,C\,t} \quad \text{..... (1)}$$

where Q = the volume of liquid deposited.
A = the cross-sectional area of the object in the plane normal to the air stream.
C = the concentration of droplets, expressed as the volume of liquid per unit volume of air.
U = the free air stream velocity, or wind speed.
t = the time the object is exposed to the stream of droplets.

The projected frontal area of a house-fly, defined as the area of a fly in normal flying posture, projected in a plane perpendicular to the line of flight, is approximately 0·10 sq. cm. Although the wings, legs and bristles are important places on which droplets are deposited, their frontal area is negligible. Droplets that are falling appreciably, relative to the air stream, tend to be deposited by settling on the horizontal surfaces of the insect, and for that reason when considering the deposition on locusts of rather larger droplets than those studied here (50–500μ dia.) Wootten & Sawyer (1954) used what they termed the Horizontal Equivalent Area as the relevant measure of locust size. As small droplets have smaller terminal velocities than larger ones, they tend to move with a more nearly horizontal trajectory, so that the inertial deposition is then of most importance, and therefore the projected frontal area has been considered here.

The droplet concentration is not easily measured directly, and the collection efficiency was therefore measured by comparing the deposit on a single fly with the deposit on the first-stage slide of a cascade impactor when each was exposed in turn to a cloud of droplets that was approximately uniform (see Table II), moving at a fixed speed in a horizontal wind tunnel. Using equation (1) for each object we have,

$$E = \frac{E}{E_c} E_c = \frac{Q}{Q_c} \cdot \frac{A_c}{A} \cdot \frac{t_c}{t} \cdot E_c \quad \text{..... (2)}$$

where the subscript c refers to the cascade impactor. All the ratios on the right-hand side of equation (2) can be measured. E_c was obtained from some recent measurements by May (1956) assuming the results obtained when sampling at 17½ litres per min. in a 3 m.p.h. wind would apply when sampling at 10 litres per min. in a 1 metre per sec. wind, the wind speed used in the present experiments.

TABLE I.

Wind speed (in cm. per sec.) at different points in the working section of the wind tunnel.

	Left*			Right*	
	2″	1″	Centre	1″	2″
2″ Up	101	105	115	105	102
Centre	105	97	91	107	107
2″ Down	111	111	105	102	97

* Viewed from upwind.

Experimental Method.

A perspex wind tunnel with a working section 1 foot in diameter was used. A spinning-top sprayer (May, 1949) situated 3 ft. upwind of the working section produced a cloud of uniformly sized droplets, but disturbed the airflow somewhat. To minimise this, a coarse wire gauze was placed immediately downwind of the sprayer. The characteristics of the airflow at different points in the working section are shown in Table I, the data in which were obtained by using a shielded hot-wire anemometer (Simmons, 1949).

The variation of the droplet cloud concentration in space was found by exposing the cascade impactor at various positions across the working section, and

TABLE II.

Variations in concentration of droplets in the wind tunnel (arbitrary units).

	1″ Left	Centre	1″ Right
½″ above centre	18	14	20
½″ below centre	20	17	19

measuring the dyed spray deposit colorimetrically, using a Unicam Absorptiometer. The results of one of these tests using droplets of 35μ dia. is shown in Table II. The deposit " shadow " is associated with the wind " shadow ", partly because less air carried less droplets. The concentration also varied during the series of tests, ranging $\pm$11 per cent. about the mean value.

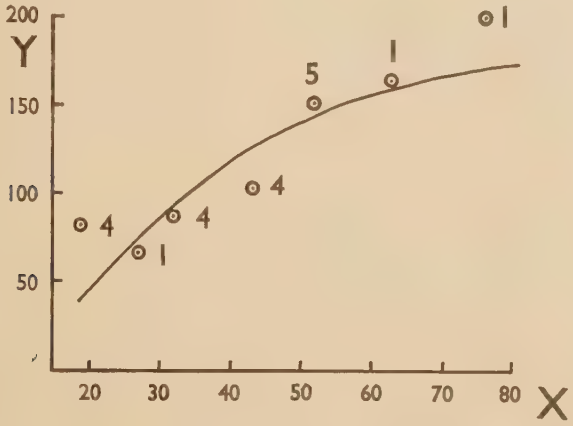


Fig. 1.—The collection efficiencies of a dead house-fly and of a sphere of 5 mm. diameter for droplets of different sizes.

X: Diameter of droplets in microns.

Y: Collection efficiency (per cent.).

Points: Measured values for single dead house-flies (based on the number of sets of exposures shown adjacent to each point).

Curve: Calculated values (×2) for a sphere of 5 mm. dia.

The oil used in the tests was that commercially known as Kerosene Extract Bottoms (density 0·928g. per cc.), and it was dyed with 8 per cent. grassol blue. The uniform oil droplets were produced by feeding the spinning top at 1–2 cc. per min. Their size was varied between approximately 20 and 75μ diameter by altering the speed of rotation of the top, and determined by exposing a magnesium-oxide coated glass plate (May, 1945, 1950) in the first stage of the cascade impactor, and measuring the pits produced under a low-powered microscope. Dead house-flies were placed singly in the centre of the wind tunnel and held in a normal flying posture, with wings outstretched, by a pin through the body. The ratios on the right-hand side of equation (2) were each measured, the quantities deposited being found by washing off the dye deposited with petroleum ether and comparing these, using a Unicam Absorptiometer. The periods of exposure, which were adjusted so that Q and Q would be similar, were 10–20 min. per fly and 1–2 min. for the cascade impactor.

Twenty sets of exposures were made in a wind of one metre per second, which Thompson (1953) found to be the average wind speed in observations made in woodland infested by tsetse fly (*Glossina*) in East Africa. In each set, two fly exposures and three cascade-impactor exposures were made in the sequence impactor–fly–impactor–fly–impactor. Mean values of the collection efficiency at various droplet sizes were computed and are plotted as points in fig. 1. The number of sets of exposures are given next to each point.

Discussion.

The deposition of droplets on to the large horizontal area of the body and wings by sedimentation, and of the droplets on to the front of the insect by inertia, together produce a collection efficiency, as defined by equation (1), that exceeds 100 per cent. in the case of the larger droplets.

These results were compared with the collection efficiency of an isolated sphere of given diameter ranging from 3–6 mm., computed using the methods described by Ranz & Wong (1952) and Langmuir & Blodgett (1945). It was found that the collecting efficiency of a fly approximated to twice the collecting efficiency of a sphere of 5 mm. diameter (shown by the curve in fig. 1), which has a cross-sectional area approximately twice the projected frontal area of a fly. No physical significance is attached to this result, but it provides a simple rule for computing the collection efficiency of flies.

Possible errors that arise include the amount of dye absorbed into the insect, but this was found to be negligible. A more serious one is that although atmospheric turbulence might affect the results slightly, a flying insect will change the airflow appreciably. This probably imposes the most severe limitation on the usefulness of these measurements on dead flies.

Considering the flying insect in woodland, we need to know the filtering effect of the vegetation and the proportion of insecticide that will be deposited on the insect. The latter is given by fig. 1, which shows that the amount deposited increases with droplet size. However, the filtering effect of the vegetation also increases with droplet size. The deposition of droplets on various objects may be calculated assuming ideal fluid-flow conditions, using the theoretical studies of Langmuir & Blodgett (1945) and others. Wind-tunnel studies by the writer (Jarman, 1959) using droplets, and by Gregory (1951) using spores of *Lycopodium*, show that the collection efficiencies due to inertia measured for cylinders and spheres are close to the theoretically calculated values if the droplet or spore adheres firmly to the object it strikes. If sedimentation is also appreciable, the deposit is increased by droplets settling on the top surfaces of the object. If the filtering effect caused by the deposition of droplets on vegetation is calculated in this way, we find that twigs smaller than 2 mm. dia. filter out more than 50 per cent. of droplets greater than 30μ dia., and twigs as large as 1 cm. dia.

filter out 50 per cent. of the droplets greater than 50μ dia. that approach them within the projected frontal area of the elements of the vegetation in a wind of 1 m. per sec. Taking a figure intermediate between these two values as representing a droplet size appropriate to a generalised pattern of vegetation, an upper limit of droplet diameter of 40μ would seem desirable if vegetation is to be penetrated. On the other hand, for deposition on the insects, droplets having a diameter of at least 20μ are desirable. The optimum range of the droplet size for the control of flying insects in woodland thus appears to be 20–40μ dia.

Summary.

An experimental laboratory study of the deposition of droplets on dead house-flies (*Musca domestica* L.) was made, using a spinning-top sprayer to produce a spray of uniformly sized oil droplets and a cascade impactor to measure the concentration of the spray of droplets, which were dyed. The deposits obtained on a dead house-fly and a cascade-impactor slide when these were exposed in turn to a wind of 1 m. per sec. in a wind tunnel were compared colorimetrically, and determinations thus made of the collection efficiency of the flies, defined as the volume of liquid deposited on an object expressed as a percentage of the volume that would have passed through the same cross-section as the object had that not been there.

The measured collecting efficiency of a fly varied from about 70 per cent. (droplet dia. 27μ) to about 200 per cent. (droplet dia. 75μ), and was approximately twice that of a sphere with a cross-sectional area twice the projected frontal area of the fly. From theoretical calculations of the filtering effect of different elements of the vegetation, it is concluded that the optimum droplet diameter for deposition on flies in woodland is 20–40μ.

Acknowledgements.

This work was carried out when the writer was on the staff of the Colonial Insecticides Research Unit, at Porton. He would like to thank Mr. D. Yeo and Dr. A. B. Hadaway for suggesting this investigation and Mr. P. T. King for his assistance with the experiments. The studies, which were directed by the Colonial Pesticides Research Committee, were financed from the Colonial Development and Welfare Fund.

References.

Green, H. L. & Lane, W. R. (1957). Particulate clouds: dusts, smokes and mists.—425 pp. London, Spon.

Gregory, P. H. (1951). Deposition of air-borne *Lycopodium* spores on cylinders. —*Ann. appl. Biol.* **38** pp. 357–376.

Jarman, R. T. (1959). The deposition of wind-borne oil droplets on spheres.— *J. agric. Engng Res.* **4** (in press).

La Mer, V. K. & Hochberg, S. (1949). The laws of deposition and the effectiveness of insecticidal aerosols.—*Chem. Rev.* **44** pp. 341–352.

Langmuir, I. & Blodgett, K. B. (1945). Mathematical investigation of water droplet trajectories.—*Gen. Elect. Res. Lab. Rep.* no. R.L. 225. Schenectady, N.Y.

Latta, R. & others (1947). The effect of particle size and velocity of movement of DDT aerosols in a wind tunnel on the mortality of mosquitoes.— *J. Wash. Acad. Sci.* **37** pp. 397–407.

May, K. R. (1945). The cascade impactor: an instrument for sampling coarse aerosols.—*J. sci. Instrum.* **22** pp. 187–195.

May, K. R. (1949). An improved spinning top homogeneous sprayer.—*J. appl. Phys.* **20** p. 932.

May, K. R. (1950). The measurement of airborne droplets by the magnesium oxide method.—*J. sci. Instrum.* **27** p. 128.

May, K. R. (1956). A cascade impactor with moving slides.—*A.M.A. Arch. industr. Hlth* **13** pp. 481–488.

Ranz, W. E. & Wong, J. B. (1952). Impaction of dust and smoke particles on surface and body collectors.—*Industr. Engng Chem.* **44** pp. 1371–1380.

Simmons, L. F. G. (1949). A shielded hot-wire anemometer for low speeds.—*J. sci. Instrum.* **26** p. 407.

Thompson, B. W. (1953). Aircraft applications of insecticides in East Africa. III. Atmospheric turbulence in woodland.—*Bull. ent. Res.* **44** pp. 611–626.

Wootten, N. W. & Sawyer, K. F. (1954). The pick-up of spray droplets by flying locusts.—*Bull. ent. Res.* **45** pp. 177–197.

© Commonwealth Agricultural Bureaux, 1959.

SOME FACTORS AFFECTING BREEDING AND OVIPOSITION OF THE RED LOCUST, *NOMADACRIS SEPTEMFASCIATA* (SERV.).

By P. Symmons and A. J. M. Carnegie

(Plates V & VI.)

The red locust, *Nomadacris septemfasciata* (Serv.), is known to exist perennially in large numbers in a few areas and it is considered that a plague can start only when swarms escape from these outbreak areas, of which the most important are the grassy plains surrounding Lake Rukwa, in south-west Tanganyika. Swarms are most likely to leave the outbreak areas when the locust population is large. Thus, in order to prevent the formation of swarms, the escape of which could start a plague, it is necessary to keep down locust numbers. Control of the numbers is being achieved successfully by spraying poison from aircraft, but this requires a permanent staff with expensive equipment capable of dealing with the heaviest outbreaks. A form of ecological control is desirable that would stabilise locust numbers at a low level and so reduce the need for chemical control. This might be achieved by altering the environmental conditions so that highly successful breeding would never occur. Alternatively, by ecological methods, the locusts might be induced to concentrate more effectively, so making chemical control easier and cheaper.

In order to decide whether or not ecological control is possible, it is necessary to know what factors affect the breeding of the red locust, for it is in the breeding season that the fastest change in numbers occurs. The main factors, which are not entirely mutually exclusive, would seem to be climate and weather, soil

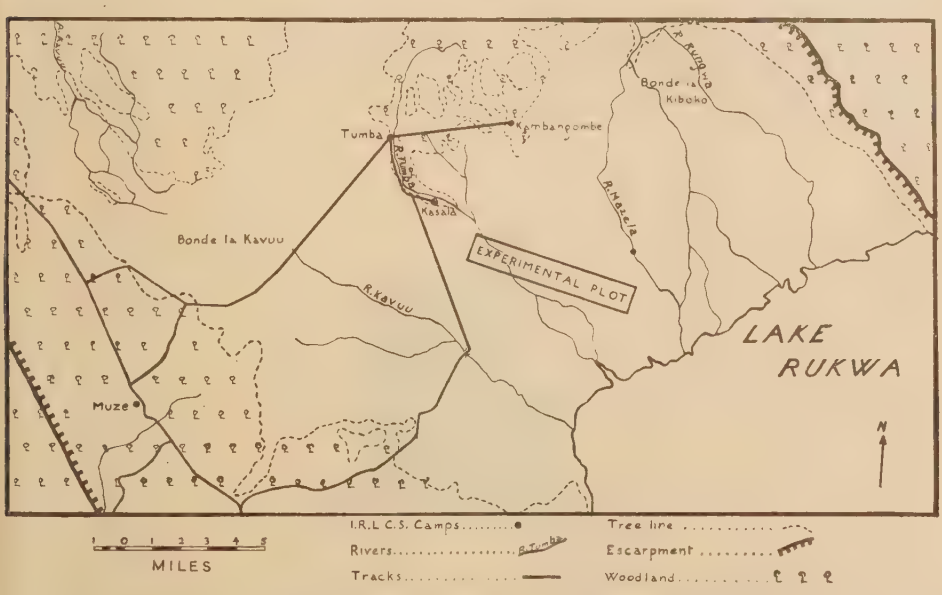


Fig. 1.—Map of North Rukwa, Tanganyika, showing position of experimental plot.

condition, type of grass and condition of the grass cover. Of these, only the condition of the grass cover can be altered with comparative ease. By protecting the North Rukwa plains (fig. 1) from fire since the beginning of 1955, an attempt has been made to alter the physical condition of the grass cover.

Experimental Fire Control in North Rukwa.

Various forms of controlled grass-burning, as a means of influencing locusts, have been tried in the past. Michelmore (1947) mentions the burning, during a dry spell in the rains, of odd bands of hoppers that had marched into patches of dry grass remaining from the previous season. In the same paper he mentions a proposal to protect the grasslands from fire until September, and then attempt to burn the roosting adults at night. Grass-burning has also been used in largely unsuccessful attempts to concentrate adult locusts for chemical control.

Some mention has been made also of the effect of fire prevention on the grasslands themselves and on succession (Backlund, 1956; Vesey-FitzGerald, 1957).

As the result of a large-scale experiment planned by Vesey-FitzGerald in 1954 and implemented in 1955, a great part of the grasslands of North Rukwa (fig. 1) have now (1958) been protected from fire for three years. The object of the experiment was to prevent dry-season fires in the grasslands and so preserve the year's accumulation of grass. If left unburnt, the grass dries and falls over, and so forms a dense cover above the ground. The general belief has been that locusts prefer to lay on bare soil in the presence of standing grass (Burnett, 1951), and it was thought therefore that the presence of a grassy mat might influence the choice of oviposition sites (Vesey-FitzGerald, 1955*a*). The presence of thick standing grass along the edge of burnt-over ground, and the fact that there were considerable numbers of locusts present there at the time of egg-laying, offered a good opportunity in 1957–58 for experimental investigation of choice of oviposition sites.

The Topography and Climate of the Rukwa Valley.

The Rukwa Valley is a rift, aligned approximately north-west to south-east, about 30 miles wide and with no drainage outlet. The main locust-breeding plains are areas of almost completely flat grassland surrounding the shallow, saline Lake Rukwa. North Rukwa lies north-west of the lake and its vegetation has been described by Vesey-FitzGerald (1955*b*).

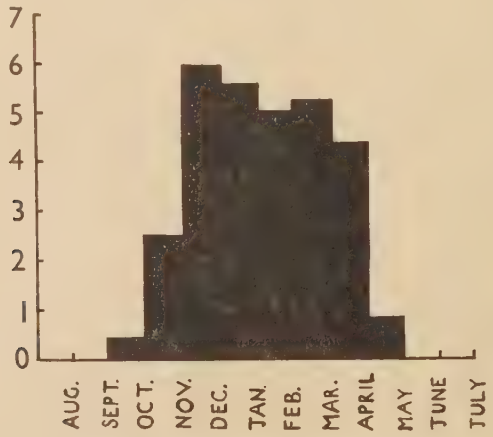


Fig. 2.—Rukwa Valley. Mean monthly rainfall (in.).

The year is divided into a single well-marked wet season and a dry season; the former lasts at the most from November to May inclusive (fig. 2), during which an average of 31 in. of rain falls over the valley floor. October and November are the hottest months and June and July the coldest (mean monthly temperatures 85, 84, 74 and 75°F., respectively) (fig. 3). The greatest mean

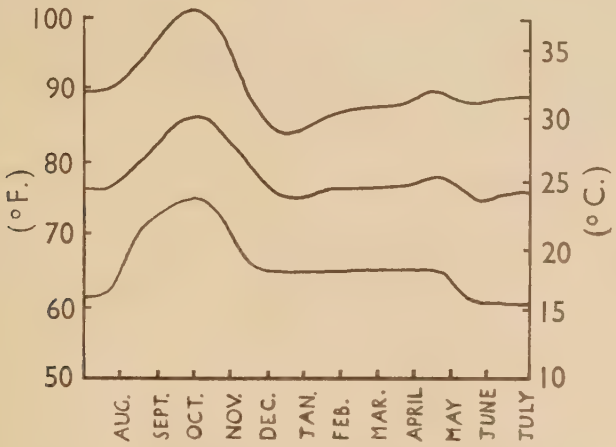


Fig. 3.—Rukwa Valley. Mean monthly temperature.

diurnal range, in July, is 31°F.; this is greater than the annual mean monthly range (11°F.). The steep south-west escarpment receives a much higher rainfall than the valley floor and over the drainage basin, which is five times as large as the valley proper, the average rainfall (36 in.) is greater than that over the valley floor.

During the wet season the plains may be dry, waterlogged, or covered with standing water varying in depth from a few inches to several feet. Standing water is found, especially, late in the season in the large " soaks " (*bonde* on map) into which the Rungwa and Kavuu rivers drain (fig. 1). It seems likely that both rain and river water contributes significantly to the size of Lake Rukwa and to the water on the plains.

The Life-cycle of the Red Locust in Outbreak Areas.

Locusts transform to the adult stage in the latter half of the rainy season, usually beginning in mid-February. They exist as immature adults throughout the dry season, during which time they may form swarms and migrate. Copulation and egg-laying begin with the first rains, in November or December, and continue for some weeks. Few, if any, adults survive after January. The incubation period of the eggs is about four weeks and the first hoppers appear usually before the end of the year; the new adults appear about two months after hatching of the eggs. More detailed descriptions may be found in Faure (1935) and Burnett (1951).

Aims and Methods of the Main Experiment.

The aims of the main experiment were to investigate the conditions (temperature, soil moisture, soil temperature and rainfall) in which eggs are laid and incubated; the effect of variations in these factors on oviposition and incubation success; and the effect on choice of oviposition site and on incubation success of

the type and condition of grass (whether burnt during the wet season, or during the dry season, or left unburnt).

Layout of the experimental plot.

The original plan was to burn a $\frac{1}{4}$-mile strip from Kasala Camp south-eastwards to near the lake shore (fig. 1). This plot was in fact marked out and much preparatory work was done, but a fire, started accidentally at the camp on the Mazela river on 28th August 1957, burnt out a large triangular block and, in view of its proximity to the projected plot, it was decided to use an area along part of the edge of this block for the work. The grasses in this new area were less varied than in the plot originally selected, but the new plot had the advantage of having been taken completely at random.

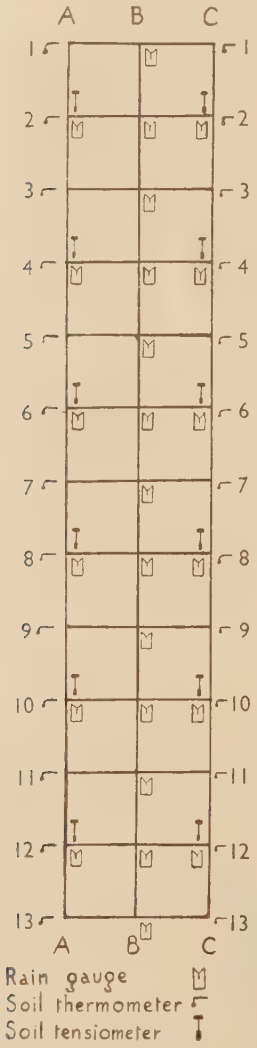


Fig. 4.—Layout of experimental plot.

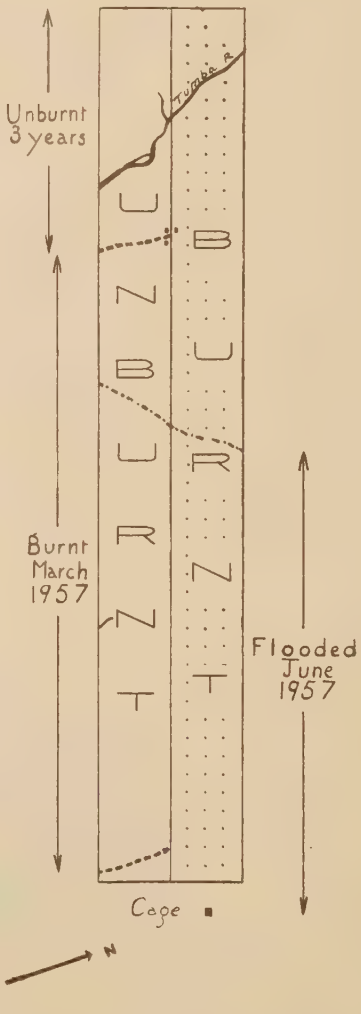


Fig. 6.—Features of experimental plot.

A straight fire-break was constructed, using the existing edge of the burn where possible, this line being tidied up by further, controlled, burning. A straight edge was thus obtained that extended for six miles. Numbered beacons were set up at half-mile intervals along the edge of the burn (B 1–13) and along lines parallel to and half a mile distant from it in the standing grass (A 1–13) and the burnt area (C 1–13) (see fig. 4). The actual edge of the original burn was used from B5 to B13; this did not deviate from the central straight line by more than 30 yd. To the west of B5 the edge of the original burn lay to the north of the straight line B5–13, and accordingly an extension of this line was mown through the standing grass from B1 to B5, using a brush cutter; this swathe was harrowed and scraped clean with a grader and the standing grass to the north of it then burnt (Pl. V, fig. 1). This controlled burning was carried out on 24th and 27th September, about a month after the original burn.

Rain gauges were set up at each beacon on the centre line (B) and at the even-numbered beacons on the side lines A and C; at the latter, Gallenkamp soil tensiometers were also installed, being sunk so that the middle of the porous pot was at a depth of about 2½ in. At each beacon of the A and C lines, a soil thermometer was sunk with its bulb 2 in. below the soil surface. All these instruments were read daily, from 19th November 1957 until 25th February 1958, the soil-thermometer readings being taken in the early afternoon, when soil temperature would be near its maximum and not changing rapidly.

The vegetation of the experimental plot.

Careful vegetation profiles were made along the A, B and C lines, the last-named being examined after the first rains had caused a re-growth of grass in the burnt-over area. From these a generalised profile was drawn (fig. 5).

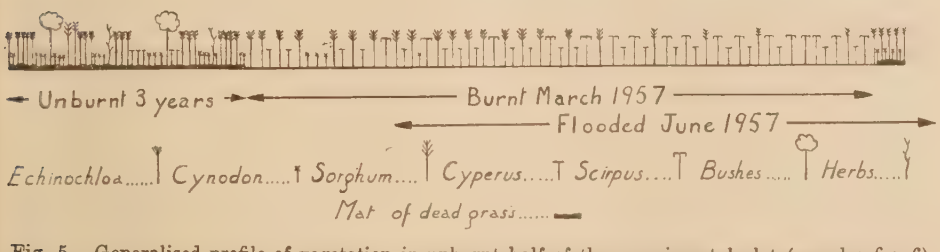


Fig. 5.—Generalised profile of vegetation in unburnt half of the experimental plot (see also fig. 6).

The plot extended from near a piece of open woodland in the west to near the Mazela river in the east, and covered quite a large variety of typical outbreak-area grasslands (Vesey-FitzGerald, 1955*b*). Over the westernmost quarter of the plot the grass was very thick, and had been protected from fire since 1954 (see fig. 6). The dominant grass in this area was *Echinochloa pyramidalis*, but patches of *Cynodon dactylon* were common, and patches of *Sorghum verticilliflorum* and of the sedge *Cyperus longus* also occurred. The Tumba river flowed through the western end, and in its immediate vicinity supported a dense growth of *Vossia cuspidata*. Scattered individually and in patches among the thick grass were the following dicotyledonous herbs and small bushes:—*Crotalaria ochroleuca*, *Crotalaria* sp., *Phaseolus mungo*, *Aeschynomene indica*, *Sesbania tetraptera*, *Alysicarpus rugosus*, *Glycine borianii*, *Rhynchosia micrantha*, *Corchorus triloculares*, *Hibiscus panduriformis*, *Pavonia* sp., *Micrococca mercurialis*, *Tragia cannabina*, *Celosia argentea*, *Striga forbesii*, *Ipomoea aquatica*, *Leucas martinicensis*, *Kedrostis foetidissima*, *Melothria madaraspatana*, *Aspilia latifolia*, *Conyza aegyptiaca*, *Pulchia dioscordis*, and *Sonchus exauriculatus*. In many parts of

the plains these dicotyledons are common near the tree-line, and there is some evidence that with protection from fire they are extending into the plains. Towards the tree-line there were occasional *Acacia* spp., and *Borassus* and *Hyphaene* palms.

Within the plot and about 1½ miles from the western end, the thick unburnt grass was replaced by grassland that had been burnt over on 18th–19th March 1957, during a dry spell that had interrupted the wet season. The general cover in this grassland was relatively sparse. *Echinochloa pyramidalis* and *Cyperus longus* were common, with *Scirpus maritimus* becoming very common towards the eastern end. Patches of *Cynodon dactylon* occurred, but became less and less common towards the eastern end. Dicotyledonous herbs and bushes were almost completely absent from this area; their absence accentuated the line of contact with the western section, unburnt for three years, in which they were prominent (see Pl. V, fig. 2). Although the growth of *Cyperus longus* and *S. maritimus* appeared normal, that of *E. pyramidalis* appeared to have been impaired as a result of the wet-season fire. The average height of the inflorescences above the ground was little less than normal, but it was clear that the ground cover was very much less than in the unburnt section. Late wet-season flooding had covered the eastern half of the plot, and may well have stimulated growth of the sedges, but not of *Echinochloa*. The flooding had extended from beyond the eastern end of the plot to within about one mile of the line of contact with the western section (see fig. 6), and it was in the flooded area that *S. maritimus* became very common. In some places the sedges intermingled with *Echinochloa* as a homogeneous mixture, and in other places *Cyperus* and *Echinochloa* formed mosaics, while occasionally *Scirpus* appeared almost as a pure stand. *Ipomoea aquatica* was also common in parts of this area.

This area of relatively sparse grassland extended for about four miles, nearly to the end of the plot, where it terminated in thick *Echinochloa*, with occasional *Cynodon*, at the easterly limit of the March fire. At this contact there was a very marked drop in the amount of *Scirpus maritimus*, and *Cyperus longus* also was less conspicuous.

The experimental plot, therefore, could be divided into the following areas (fig. 6):—

(1) An area burnt off thoroughly in the latter part of the dry season (between B–B and C–C).
(2) An unburnt area of four years' accumulated growth that had not been flooded.
(3) An area of standing grass regenerated after a damaging fire during the previous wet season, of which a large part had been flooded after the fire.
(4) A small unburnt area of four years' accumulated growth that had been flooded in the previous wet season.

Observations on Locusts during the Experiment.

On 9th–10th October 1957 a thorough assessment of the locust population was carried out by Land-Rover, using the method described by Scheepers & Gunn (1958). On 18th November the first light rain fell on the south-east part of the plot, but had no apparent effect on either the locusts or the grassland. Heavy rain set in on 6th December and an average over the plot of 4·0 in. fell in the six days from 6th to 11th December. Mr. Vesey-FitzGerald reported that there was "a general post" with locusts "streaming out" of the standing grass to lay eggs in the burnt area.

On 16th and 17th December, assessments of adult locust populations by both foot and Land-Rover methods were carried out and a final assessment of adults was made on foot on 6th January 1958.

From 30th December to 14th January a systematic search was made for locust

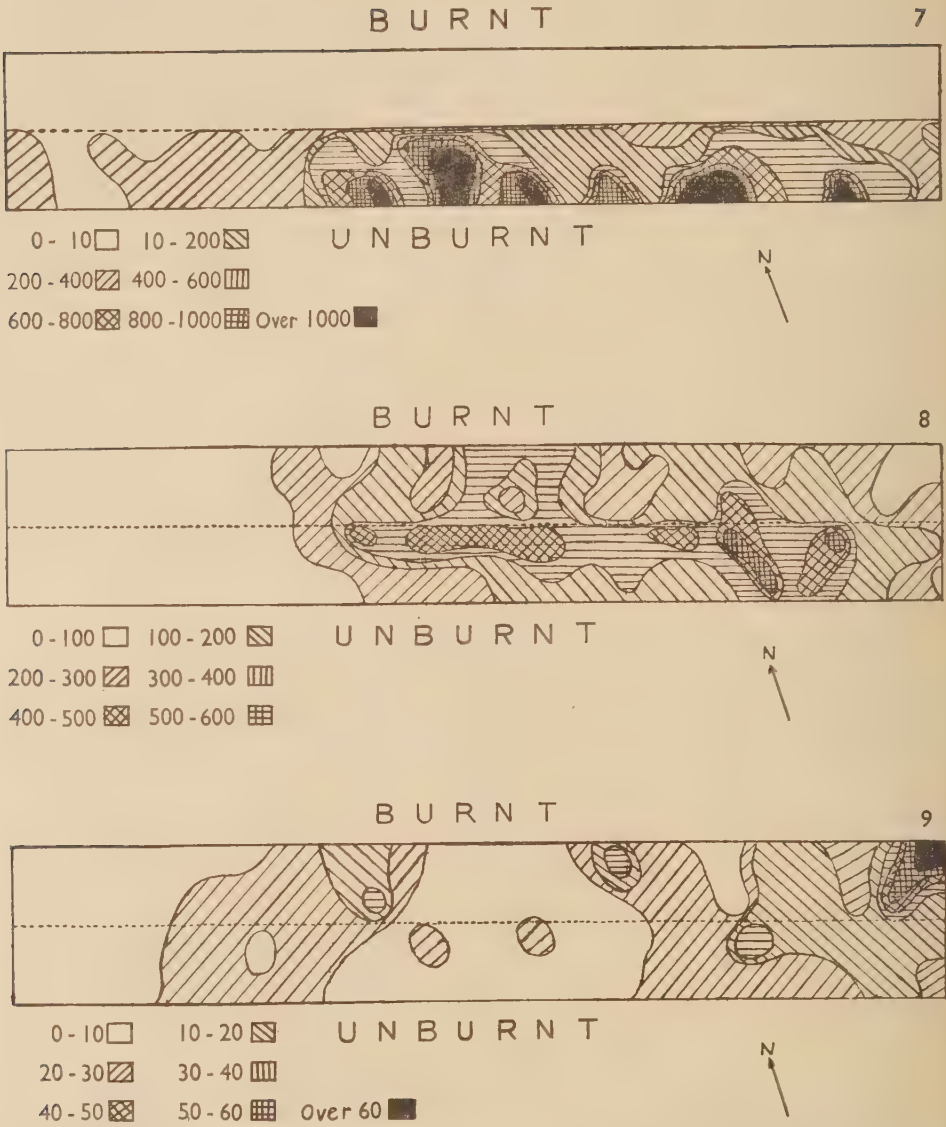
egg-pods. Ten parallel strips, each 200 yd. long and about four feet wide, with a space of about five yards between adjacent strips, were mown near each centre-line beacon (B1–13; see Pl. VI, fig. 1). The strips were at right angles to the line of contact between the burnt-over and unburnt areas and extending equally into each sector. A single furrow was ploughed along the middle of each strip, and a team, consisting of five labourers under a senior African, searched it for locust egg-pods, inspecting the cut and breaking up the overturned soil (Pl. VI, fig. 2). Near each of the side-line beacons (A1–13 and C1–13), a set of five strips, 200 yd. long, within and parallel to the edge of the plot, were similarly mown, ploughed and searched. Each set of strips started about 20 yd. north-west of the beacon, to reduce the risk of damage to the meteorological instruments. In addition, parallel to, and to the south-east of, the line joining beacons A10, B10 and C10, five strips were mown and ploughed from one side of the plot to the other, a distance of one mile; these were searched for locust egg-pods, and the distance from the central line was measured for each pod found.

The first hoppers were seen on 3rd January 1958. Assessments of hopper populations were carried out on 7th and 8th; 16th, 17th and 18th; 20th, 21st and 22nd; and 24th, 25th and 27th January. The method used was for two African scouts to walk through the grass, which by mid-December had put out fresh growth in all areas of the plot, one counting every pace, and the other counting the number of paces taken through grass in which hoppers occurred. The number of paces taken through infested grass was noted for each successive 100 paces walked, and the degree of infestation thus expressed as a percentage.

Adult locusts.

The assessments of adult locust populations were carried out on a series of parallel lines and a standard error for the total population was calculated by the method given by Yates (1949) for systematic samples. As has been pointed out (Scheepers & Gunn, 1958), because of the "clumpy" nature of locust distribution, a standard error cannot be calculated by the usual method. It is possible that, using methods of assessment either by Land-Rover or on foot, certain systematic errors occur. Both methods assume that, provided the assessment is carried out in the prescribed manner (Scheepers & Gunn, 1958), a constant proportion of the locusts is flushed. During the course of the dry season the physical state of the grassland changes, locust behaviour may also change, and it is not known how, if at all, these changes affect the proportion of locusts flushed during assessments. A further source of error is introduced by the use of assessments both on foot and by Land-Rover. This was unavoidable since the ground became impassable to Land-Rovers in late December. A conversion factor for assessments on foot was worked out on the basis of the work of mid-December, when both methods were used. These criticisms apply mainly to a comparison between assessments at different times and not to estimations of the differences in the distribution of locusts within the plot on a given occasion.

The total population of adult locusts in the plot at the October assessment was 398,000 $\pm$ 41,000 (fig. 7); by mid-December, after the start of egg-laying, there were 344,000 $\pm$ 24,000 (fig. 8). This difference is not significant ($P = 0{\cdot}4$). By early January, after the main laying period, the numbers had fallen to 33,500 $\pm$ 3,200, showing a highly significant ($P < 0{\cdot}01$) and very rapid decrease in the size of the population (fig. 9). It should be noted, however, that the observation plot was not entirely self-contained; in mid-December, adult locusts were flushed in the burnt-over area south of Kambangombe (fig. 1), where there had been no locusts before the first rain. It is almost certain that these adults came from the plot or from the standing grass to the south-west of the plot, since a routine assessment, carried out by the control staff of the Service in November, did not reveal any other concentration of adult locusts in the North Rukwa plains. It



Figs. 7–9.—Distribution and density of adult locusts in experimental plot at various dates.

Fig. 7.—9th–10th October (before egg-laying). Number of locusts, 398,000; scouting intensity, 5·6 miles per sq. mile.

Fig. 8.—16th–17th December (during egg-laying). Number of locusts, 344,000; scouting intensity, 7·1 miles per sq. mile.

Fig. 9.—6th January (after main egg-laying). Number of locusts, 33,500; scouting intensity, 2·8 miles per sq. mile.

The figures express locust density as adults per 10,000 sq. yd.

seems likely, however, that the movement of locusts out of the plot to the north-east was more or less balanced by a movement into the plot from the south-west.

In mid-December a considerable number of dismembered locusts was seen on the burnt ground; these were probably killed by birds, possibly whilst in the act of laying (Vesey-FitzGerald, 1955*c*). It seems obvious, however, that the main drop in population size occurred between 16th December and 6th January. The reason for this drop is not known, but it is quite usual. Emigration could scarcely be the cause, since locusts were not seen to move out of the area or to increase in numbers greatly elsewhere. It seems likely that at this time the adult locusts died either following oviposition or because of the seasonal change in the weather.

Considering the distribution in mid-October (fig. 7), firstly it can be seen that locusts were completely absent from the recently burnt-over ground (mean number of locusts per 10,000 sq. yd. on unburnt area: 418 ± 52; on burnt-over ground: 0 ± 0; $P < 0{\cdot}01$) though, by the time the assessment was made, short green grass, suitable for feeding, was present. In spite of a few stalks of *Echinochloa* left after the burning, the cover on the burnt-over ground was insufficient to form a shield against the sun. Secondly, adult locusts were found almost exclusively in the standing grass that had suffered a wet-season burn (fig. 6) (mean number of locusts per 10,000 sq. yd. in grassland burnt off in the previous wet season: 588 ± 99; in grass unburnt for three years: 18 ± 5; $P < 0{\cdot}01$). It can be seen, however, from fig. 7 that the small area of grass unburnt for three years at the south-east end of the unburnt half of the plot harboured a denser population than the unburnt grassland at the north-west end. In fact, the area of most dense infestation had been largely covered by standing water late in the previous wet season. It is probable that it was the condition of the grass cover that influenced the distribution of the adult locusts; the grass in the area burnt off in the wet season was a little shorter and much sparser than that in the section unburnt for three years. Lastly, there was a tendency for the adult locusts to be most numerous, not along the line of contact of the burnt and unburnt halves of the plot, but at a distance from this contact. The mean number of locusts per 10,000 sq. yd. on $\frac{1}{4}$-mile-wide bands in unburnt grass running parallel to the line of contact (B) was as follows:

$$0\text{–}\tfrac{1}{4} \text{ mile from B} : 282 \pm 53$$
$$\tfrac{1}{4}\text{–}\tfrac{1}{2} \text{ mile from B} : 570 \pm 120$$
$$P = 0{\cdot}03$$

By mid-December, after the start of laying, this pattern had changed significantly (fig. 8). The adult locusts had spread out from the unburnt grass into the burnt-over zone. There were still few locusts in the grass that had been unburnt for three years and small numbers in the adjacent burnt-over area. At this time, there were no significant differences between the numbers of locusts on the $\frac{1}{4}$-mile-wide band adjacent to the contact line and in the burnt-off area, the band $\frac{1}{4}$–$\frac{1}{2}$ mile from the contact in the burnt-off area, and the band $\frac{1}{4}$–$\frac{1}{2}$ mile from the contact in the unburnt grass, the mean numbers of locusts per 10,000 sq. yd. in these bands being 158 ± 20, 152 ± 16, and 159 ± 22, respectively. There was an accumulation of locusts, however, in the remaining $\frac{1}{4}$-mile band, namely, that against the contact line and in the unburnt grass. The mean number of locusts per 10,000 sq. yd. in this band was 272 ± 28 (the difference from any of the other bands being $P < 0{\cdot}01$). This suggests that, with the first rains, many locusts had moved into the burnt-off area to lay eggs but that some either preferred to remain in or return to the standing grass adjacent to a burnt area, or to pause along this line before moving on to the burnt-off ground. By this time the grass in the burnt-off area had grown, so providing a certain amount of cover.

By 6th January not only had the size of the population been reduced greatly but there was no significant variation in the distribution over the whole plot (fig. 9).

Egg-pods.

The distribution of egg-pods is shown in fig. 10. The numbers of pods are those found in 1,000 yd. of plough-line; as the plough cut was 2·9 ± 0·7 in. deep and 4·6 ± 0·9 in. wide, each 1,000 yd. of furrow covered about 130 sq. yd. Though variations in the width and depth of cut occurred, there is no reason

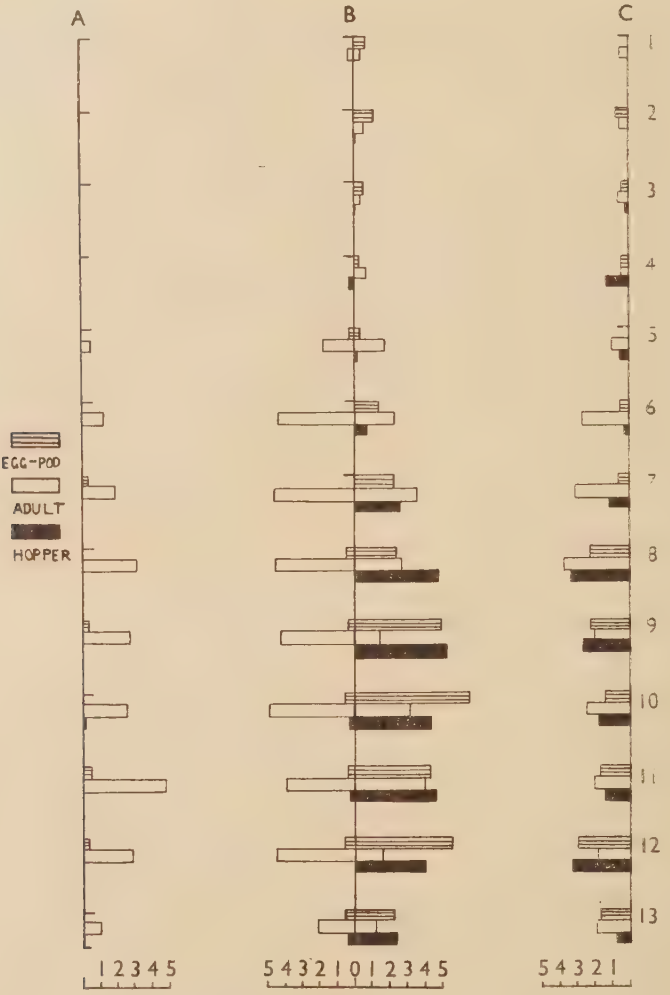


Fig. 10.—Density of egg-pods, hoppers and adults at each beacon of the experimental plot.

Scale: Egg-pods (per 130 sq. yd.)—1 scale division = 5 egg-pods.
Hoppers (percentage infestation)—1 scale division = 2%.
Adults (per 10,000 sq. yd.)—1 scale division = 50 adults.

to suppose that there was any systematic error; the grass was mown before ploughing, and variations in the grass cover would therefore have had little effect on the plough-cut.

A pod contains about 100 eggs (Robertson, 1954) and measures about half an inch across and two inches in length. It is deposited vertically with its top about one inch below the surface of the soil.

Examination of the egg-pod data (fig. 10) shows that the locusts had laid almost exclusively in the burnt-over ground. The numbers of pods found on the burnt-over and unburnt sides of the contact line (B1–13) were 147 ± 19 and 10 ± 3, respectively ($P < 0{\cdot}01$). The figures for the pods found approximately half-a-mile deep in the burnt-over ground and unburnt grassland were 71 ± 10 and 6 ± 3, respectively ($P < 0{\cdot}01$). From the total it seems likely that between 600,000 and 700,000 egg-pods were laid in the plot, or slightly more than three pods for every two locusts present within the plot at the time of the assessment of 16th December. It will be noted, however, that the contours of the highest densities in fig. 7 indicate large numbers of locusts just outside the plot to the south-west and that the distribution of egg-pods across the plot (fig. 11) suggests

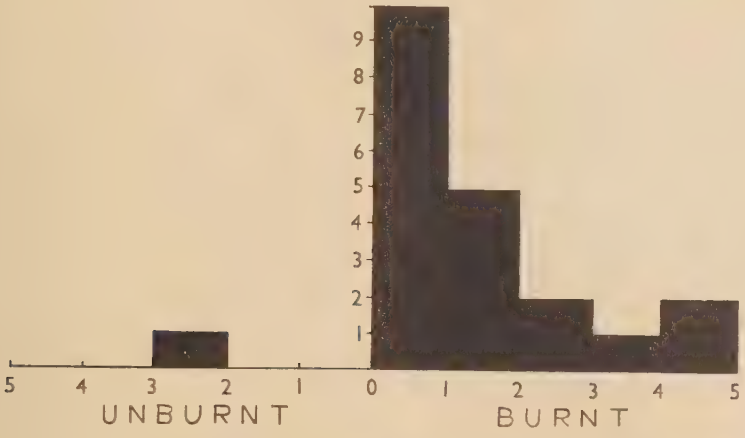


Fig. 11.—Distribution of egg-pods across the experimental plot.

Abscissae: Distance from contact between burnt and unburnt halves (line B) in tenths of a mile.

Ordinates: Number of egg-pods found in five plough lines at beacons 10.

that considerable numbers may have been laid outside the plot to north-east; consequently, no exact figure can be given for the number of egg-pods laid per female parent. During the laying period, considerable movement of adults across the line of contact of the burnt and unburnt areas in both directions was noticed. Many of the locusts in the unburnt grass must have moved on to the burnt-off sector to lay. Some may have returned to the unburnt area; but locusts were found south of Kambangombe at this time (locusts which almost certainly came from the south-west) and it is probable that there was a steady south-west to north-east movement, with adult locusts from the unburnt grass outside the plot also participating.

The distribution of the rather small number of egg-pods found, with distances measured at right angles to the line of contact (B), is shown in fig. 11 for the five traverses across the whole plot made from A10 to C10. In the burnt-off area, as can be seen, about 50 per cent. of the pods were found within 0·1 mile

of the contact line and from 0·2 to 0·5 mile the distribution was more or less uniform, probably continuing at similar densities for some distance beyond the edge of the plot.

Subsidiary cage experiment.—The data presented above show clearly that, before egg-laying, the adult locusts were found in the tall grass and not in the burnt-off area, but that the eggs were mostly laid in the burnt-off area. These observations show how the adult locusts behaved but give no information about the suitability of the tall-grass environment, as against the burnt-off one, for incubation and survival of the eggs; nor do they show whether or not the locusts will lay eggs amidst the tall grass, if given no alternative site. To test the variation in the number of pods laid by a given static parental population, three cages, each 12 ft. by 10 ft., by 9 ft. high, were constructed (Pl. V, fig. 2). The frames were of wood and were covered with ¼-inch wire mesh. Because of difficulty in obtaining the wire, the cages were not finished until mid-December. The site chosen for them was north-east of B4 at the junction of the areas burnt off early (March), late (August), and unburnt; one cage was erected in each type of grassland.

On 16th December, 40 locusts, 20 of each sex, were installed in each cage. By 15th January they had all died; the cages were then removed and each covered area was carefully searched. There were nine pods found under the cage in the lately burnt-off ground, seven in the early burnt, and four in the grass unburnt for three years. The largest of these numbers is less than one egg-pod per two female locusts and is therefore much lower than the average of between one and two per adult in the main observations. Because the cages were put down after egg-laying had begun amongst the free locusts, an area close to each cage and of the same extent was searched for egg-pods; only one pod was found, in the burnt-off zone, and the cages were in fact in a place which had had few locusts near it. We may therefore assume that the pods found under the cages had been laid by caged parental populations of equal size.

Because of the artificial conditions in the cages and because only one cage was installed in each type of grassland it is only possible to draw tentative conclusions from this experiment. Nevertheless the experiment suggested that, where there was no choice of oviposition site, the greatest number of surviving egg-pods occurred in the lately burnt-off ground, almost as many in the early-burnt area, and about half as many in the unburnt area. This could result either from variations in the number of pods laid or in pod survival. Vesey-FitzGerald (1955*a*) has suggested that the locust is reluctant to lay through an accumulated mat of dead grass. This mat was far thicker and more continuous in the unburnt than in the early-burnt area and was absent from the lately burnt-off ground. There were, however, indications that soil conditions were different under the fire-protected grass and in the burnt-off area (see below). Soil temperature was lower and the soil-moisture content fluctuated less and tended to be higher in the protected area.

A preliminary investigation was made of the soil fauna in the three areas. A soil sample was taken from near each of the three cages. The sample from the area unburnt for three years yielded the greatest number of individual organisms.

Hopper distribution.

A small isolated patch of hoppers was found on 3rd January, but scouting on 4th January failed to reveal any infested areas. By 20th and 21st January, however, scouting showed a mean infestation of 1·2 ± 0·2 per cent. (Scheepers, Eyssell & Gunn, 1958) and the population increased rapidly until 24th–27th January (infestation 2·5 ± 0·1%). The assessment of 29th, 30th, 31st January showed a mean infestation of 2·2 ± 0·1 per cent. As these last two assessments

do not differ significantly ($P = 0{\cdot}5$) they have been combined and used as an estimate of the hopper distribution (fig. 12).

An examination of this combined estimate of hopper distribution confirms the findings of the egg search. It can be seen that hoppers were found almost exclusively on the burnt-off area (infestation of burnt-off ground $4{\cdot}70 \pm 0{\cdot}25\%$, of unburnt ground $0{\cdot}05 \pm 0{\cdot}02\%$; $P < 0{\cdot}01$). Within the unburnt grass, the infestation was very low indeed, and tended to be greater in the $\frac{1}{4}$-mile band

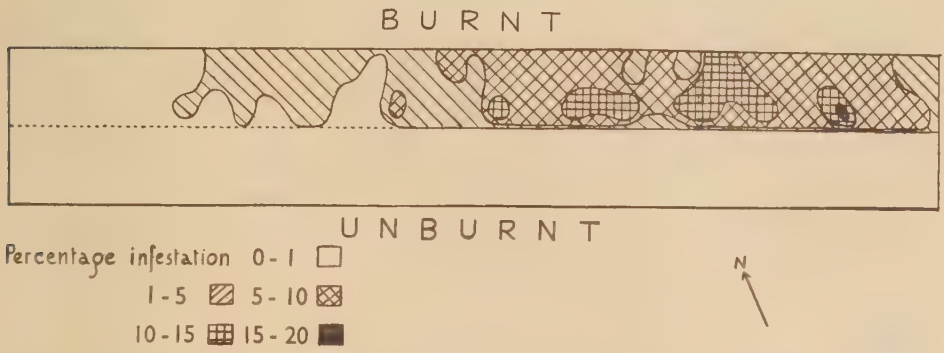


Fig. 12.—Distribution and density of hoppers in experimental plot at 24th–31st January. Mean infestation, 2·4 per cent.; scouting intensity, 15·5 miles per sq. mile.

adjacent to the contact line than in the band at $\frac{1}{4}$–$\frac{1}{2}$ mile from the contact, although the difference was not significant ($0{\cdot}056 \pm 0{\cdot}025\%$ and $0{\cdot}041 \pm 0{\cdot}024\%$, respectively; $P = 0{\cdot}7$). In the burnt-off ground, on the other hand, the infestation was significantly higher in the $\frac{1}{4}$-mile band next to the contact line than in the band at $\frac{1}{4}$–$\frac{1}{2}$ mile ($5{\cdot}3 \pm 0{\cdot}4\%$ and $3{\cdot}9 \pm 0{\cdot}4\%$, respectively; $P = 0{\cdot}01$). One feature of interest was that the number of hoppers in the unburnt grass was even lower than might have been expected from the results of the egg-pod

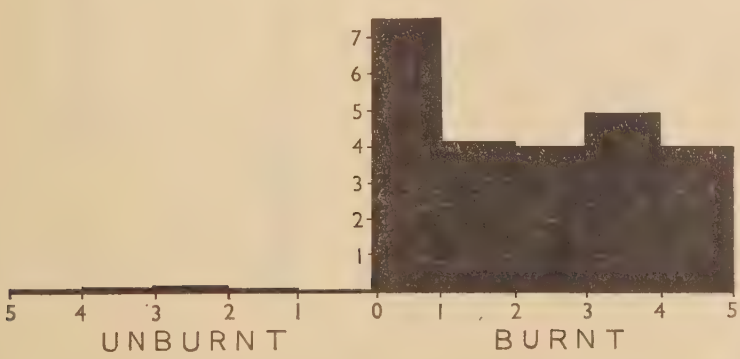


Fig. 13.—Distribution of hoppers across the experimental plot.

Abscissae: Distance from contact between burnt and unburnt halves (line B) in tenths of a mile.

Ordinate: Percentage infestation (average of traverses at each beacon).

survey. The ratio of egg-pods found in the unburnt and burnt-off areas was 0·077 : 1, whilst the ratio of percentage infestations by hoppers was 0·011 : 1 ($P < 0·01$). This result needs to be viewed with caution since:—(a) the egg-pod totals are the sum of two systematic samples taken from a population known to be stratified parallel to these sample lines; thus the totals for the two areas might be either under- or over-estimates, to an extent not allowed for by the computed standard errors, though it would seem likely that the error in both areas would be in the same sense so that the ratio is probably free from any large systematic error; (b) the method used for estimating hoppers is inadequate though a relative overestimate of low infestations is likely to result, since these might be spread over the same areas but less densely; if this in fact occurred, the discrepancy would be still greater. However, the method used over-estimates the standard error so that it is likely that the difference between the true egg-pod ratio and the ratio of hopper infestation is in fact significant. It is almost certain that fewer eggs were laid in the unburnt than the burnt-off sector; more than that, the rate of egg survival appears to have been very significantly lower under the unburnt grass than under fresh grass following a dry-season fire.

The proportional distribution of hoppers at right angles to the contact line is shown in fig. 13. This is based on the data from the assessments of 24th, 25th and 27th, and 29th, 30th and 31st January.

Ecoclimate in the Experimental Plot.

Rainfall.

The first effective rain fell on 6th December and there was a considerable fall in each day from 6th to 11th December inclusive. Two further rainy spells

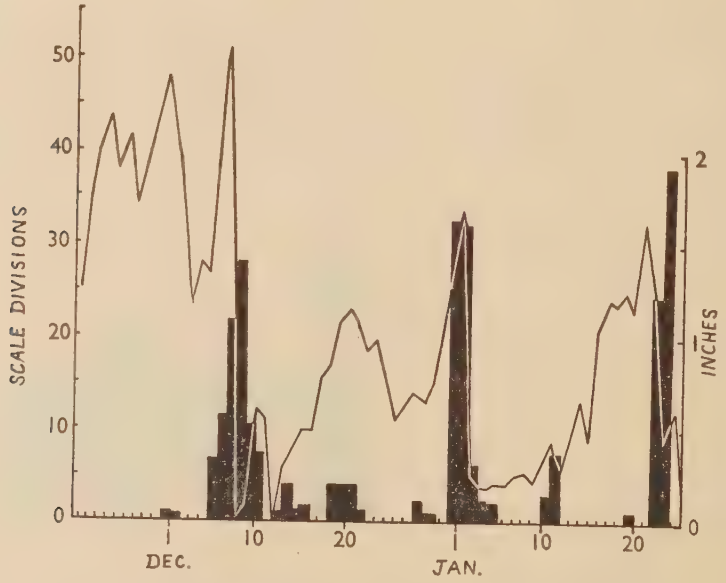


Fig. 14.—Daily readings of soil tensiometer and rainfall.

Tensiometer readings (average of 12 instruments, expressed in scale divisions)—continuous line.

Rainfall (average of 25 gauges, expressed in inches)—histogram.

occurred on 1st, 2nd and 3rd, and 23rd, 24th and 25th January (fig. 14). The mean total rainfall was 13·84 in. but this varied from place to place within the plot (fig. 15).

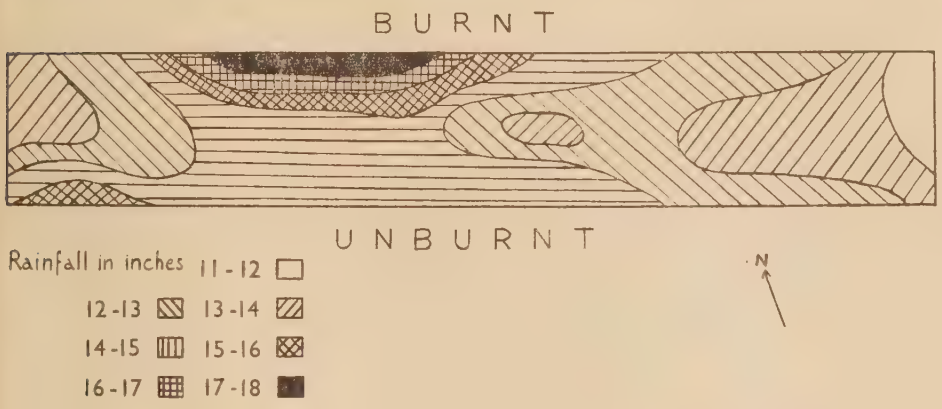


Fig. 15.—Rainfall distribution in plot (total rainfall, 19th November–25th January). Mean rainfall (from 25 gauges), 13·8 in.

Soil moisture.

The average soil tensiometer reading for the period from 8th December was 14, indicating exceedingly moist conditions. As can be seen from fig. 14, the soil, which had been excessively dry, became waterlogged as a result of the rains of 6th–11th December. The soil became slowly drier until 22nd December; the

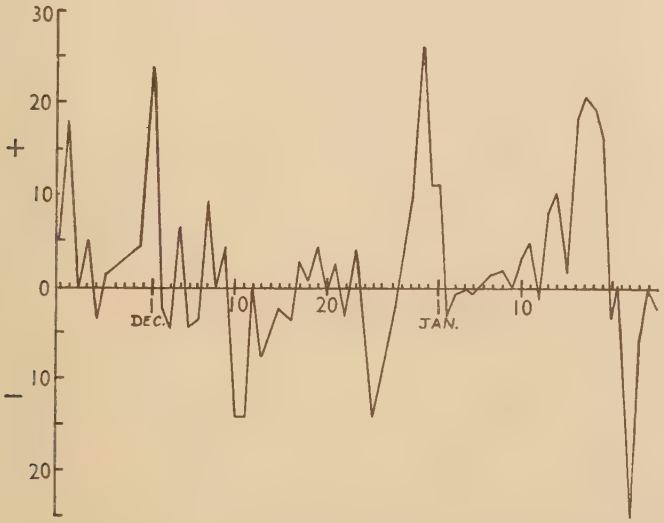


Fig. 16.—Difference in soil moisture content of burnt and unburnt ground, expressed as soil tensiometer readings (in scale divisions) in burnt ground minus readings in unburnt ground. Average of readings from six instruments in each area.

light rains of 19th and 20th December then produced an increase in soil moisture. The soil dried out again rapidly and became almost completely arid until the heavy rains of 1st, 2nd and 3rd January. Another steady decrease in soil moisture then took place, until terminated by the rainfall of 23rd and 24th January.

As can be seen from fig. 16, there was a tendency for the ground covered with standing grass to be damper than the ground that had been burnt off. The mean figures for 8th December to 25th January are 14·5 and 13·9, respectively, but the difference is small and is not significant ($P = 0{\cdot}4$–$0{\cdot}5$). If, however, we consider different kinds of weather separately instead of lumping them all together, figs. 14 and 16 suggest that under dry or drying conditions the soil under the unburnt grass was moister than that which had been burnt off, *e.g.*, 21st to 30th November, 28th December to 1st January, 14th January to 19th January. Moreover, rain appeared to affect the exposed burnt area more readily, so that immediately after heavy rain, or during a period of slight rain, the burnt-off ground was moister than the unburnt area; thus, the burnt-off ground became moister than the unburnt after the heavy rain of 8th and 9th December and remained so for much of the period from 10th to 27th December, during which there were a number of light showers; again, after the heavy rain of 1st and 2nd, and 23rd and 24th of January the burnt-off ground was moister than the unburnt.

Soil temperature.

The mean soil temperature, measured at a depth of 2 in. during the afternoon, averaged 85°F. for the period 8th December–25th January (fig. 17). The temperature was significantly higher (fig. 18) in the burnt-off ground than under the unburnt grass (86·3 and 84·7°F.; $P < 0{\cdot}01$). The temperatures were

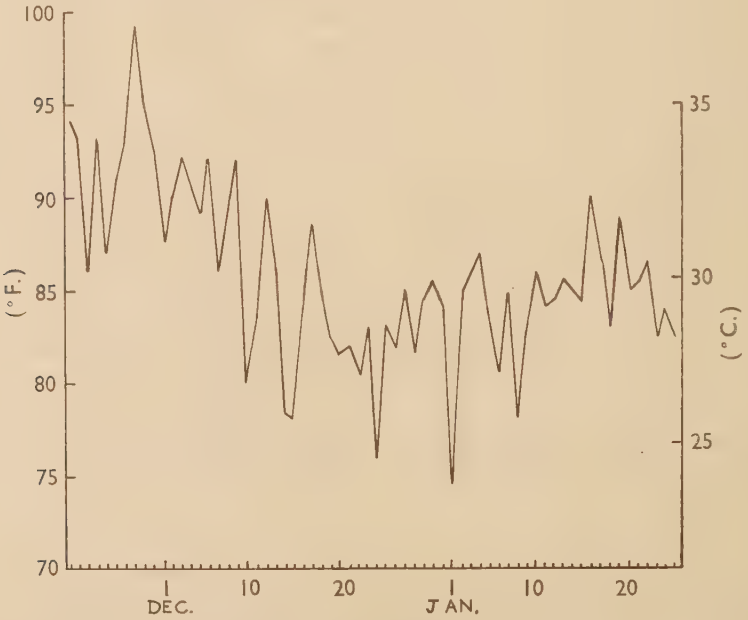


Fig. 17.—Daily soil temperatures. Average reading of 26 instruments at a depth of 2 in.

remarkably constant in the two parts of the area, the standard deviations being 0·6 and 0·9°F., respectively. The mean temperature in the burnt-off ground was 95°F. for 21st to 30th November and over 100°F. was often recorded. The

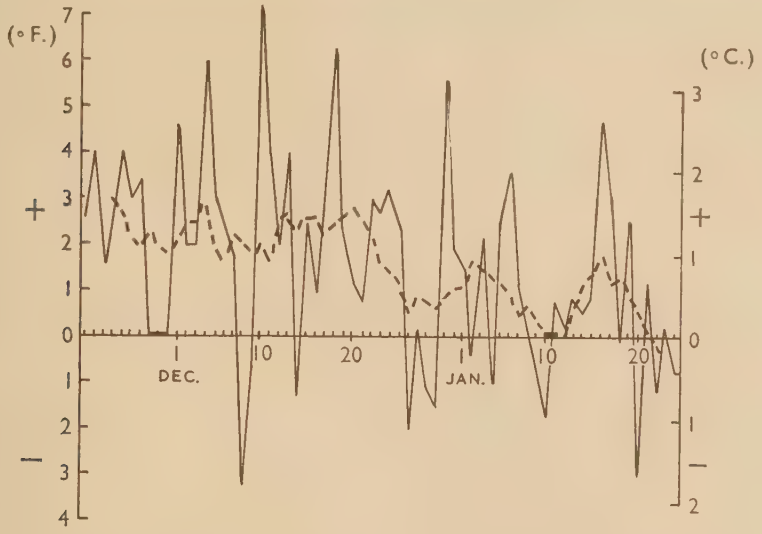


Fig. 18.—Difference between soil temperatures in burnt and unburnt ground, expressed as temperature in burnt ground minus temperature in unburnt ground. Average reading of 13 instruments in each area. Broken line represents 7-day running means.

surface-soil temperature would have been much above this and, coupled with the complete lack of cover, this could well account for the absence of locusts from the burnt-off ground. R. F. Chapman (Micro-climate in a locust habitat.—

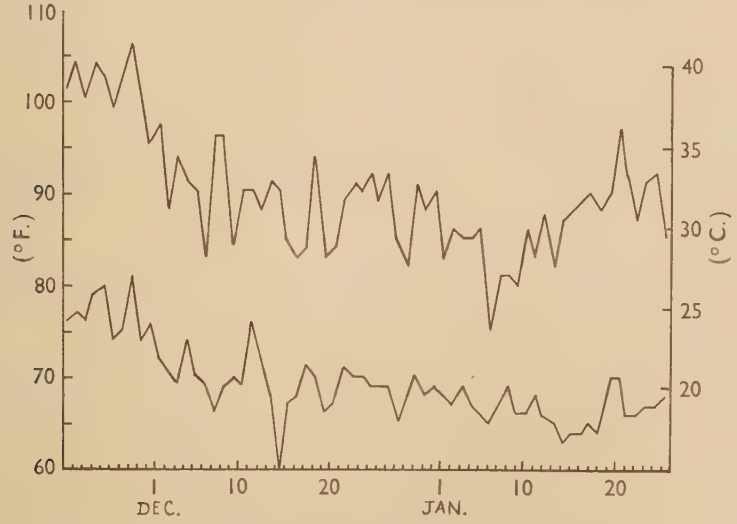


Fig. 19.—Daily maximum and minimum shade temperatures.

Unpublished, 1958) measured temperatures, on the surface of bare ground, as high as 136°F., which is far above the thermal death point for adult locusts, which he placed at about 104°F. He found also that the temperature was much less at 7·5 cm. below the surface of the ground. With maximum shade temperatures frequently over 100°F., the bare ground surface must have been hotter than the thermal death point during much of November. As can be seen from fig. 17, the soil temperature dropped at the time of the first rains and thereafter varied little; a similar pattern was displayed by the maximum and minimum air-shade temperatures (fig. 19). Ramdas & Draid (1934), working in India, showed that 0·5 in. of rain reduced surface-soil temperatures by 18°F. and that the effect persisted for four days. Not only will rain soften the soil, making oviposition easier, but it will also reduce the surface temperature so that locusts can exist on the bare ground, which is shown above to be the preferred egg-laying site. It is interesting to note that the difference between the temperatures in the burnt-off and unburnt areas became progressively less as time went on (fig. 18). This was due, probably, to the growth of grass; by 25th January the new grass was over 6 ft. high in places and thus both areas were well shaded and the effect of the old growth would have been negligible.

Relation of ecoclimatic factors to locust breeding.

As has been pointed out, there is some reason to suppose that the rate of egg-survival was lower under the unburnt grass. The rainfall did not differ significantly between burnt and unburnt areas during the incubation period, but the soil was significantly cooler by day in the latter.

An attempt was made to correlate breeding success in the burnt-off area with certain conditions during the incubation period of the eggs, namely, total rainfall, mean recorded soil temperature, and mean soil moisture. The most satisfactory criterion of breeding success in different parts of the plot is the ratio of hopper infestation to egg-pods found, in the region of each beacon. There was, however, no significant correlation between this ratio and any of the factors listed above.

Discussion.

The observations recorded here show that adults of the red locust show a marked preference for ovipositing in ground that has been burnt over in the preceding dry season. The burning of selected strips should, therefore, lead to concentration of oviposition and, consequently, of hoppers, thus making chemical control of the latter easier and cheaper. The width of strips and the distance between them that would produce the most effective concentration needs to be investigated. It is possible that complete fire-protection would produce a smaller hopper population, although the advantage of such a reduction might be offset by the scattered distribution of the resulting population, which would make chemical control difficult and expensive; this possibility, also, needs quantitative investigation.

The sequence of events that brings about oviposition on ground that has been burnt over in the preceding dry season is worth consideration. It is known that egg-laying by the red locust occurs mainly at night (Faure, 1935), though it has been seen in the day-time in dull weather (Carnegie, unpublished). It may therefore be concluded that a high soil-surface temperature during full sunshine could not be important in preventing egg-laying, because in sunny conditions the locusts do not lay eggs. It is equally clear that high ground-temperatures would confine the locusts to the unburnt grass during the day-time. Although the nights are warm enough, just before the rains begin, for the locusts to move, the ground is then hard and dry and therefore unsuitable for oviposition. Once the eggs are ready for laying, the locusts will lay in cool, moist, bare soil, and almost exclusively in such conditions. It is not, however, a set of conditions of which the

locust could be informed from a distance and evidently what must happen is that adults tend to arrive in the cool, moist, bare places by random movements. Once arrived, they can remain, for it is not too hot, the grass, now growing, provides food and some roosting places, and egg-laying can proceed. The question of interest is whether flight activity is constant over the whole period, or whether it is stimulated and increased at the time when cool, moist, bare soil becomes available. If the former is the case, then before the rain one would observe the flight activity but the hot, dry, bare soil would not retain the locusts. If the latter were the case, one might be able to discover what factor of the environment it is that stimulates activity; for example, a local temperature-drop can occur without local rain, or a slight shower may occur before the main, or any substantial, fall of temperature. Further observations are required for such an analysis of behaviour.

Summary.

Observations were made on the red locust, *Nomadacris septemfasciata* (Serv.), between October 1957 and February 1958 in an area of grassland, six miles long by one mile wide, marked out by beacons and divided lengthwise by a line of beacons down the centre, in the Rukwa Valley of south-west Tanganyika.

One half of the plot had been burnt off completely in the latter part of the dry season; the other half was unburnt and carried in part a four-year accumulation of growth and in part an area of standing grass that had regenerated after a damaging fire during the previous wet season and then, for the most part, flooded. Vegetation profiles were made along the whole length of the plot, and rain gauges, soil thermometers and soil tensiometers were installed at regular intervals along the three lines of beacons. Assessments of the population and distribution of adult locusts within the plot were made from Land-Rover or on foot in mid-October, mid-December (ten days after the onset of the rains) and early in January. A systematic search was made for egg-pods, starting at the end of December, along furrows ploughed down the middle of each of a number of narrow strips mown in the grass in sets near each beacon and sampling equally the burnt and unburnt halves of the plot. The first hoppers were seen on 3rd January, and assessments of hopper populations were carried out four times during January.

The primary object of the work was to study the effect on choice of oviposition site and on incubation success of the type and condition of the grassland (whether burnt during the previous dry season, at an earlier date, or left unburnt) and its possible bearing on control of the species in an outbreak area. Data were also obtained on the conditions of air temperature, soil moisture, soil temperature and rainfall in which eggs are laid and incubated; and the effect of variations in these factors on oviposition and on incubation success was examined.

It was observed that, in the hot, dry conditions of mid-October, adult locusts were completely absent from the recently burnt-over ground, and were found almost exclusively in that part of the standing grass that had suffered a wet-season burn. By mid-December, the locusts had spread out from the unburnt into the burnt-over zone, where the grass had put out fresh growth, but many were still to be found in the former, with a concentration along the line of contact with the latter. By early January, the size of the population had been greatly reduced and it was evenly distributed over the whole plot.

The distribution of egg-pods showed that the locusts had laid almost exclusively in the burnt-over zone, about 50 per cent. being found within 0·1 mile of the line of contact with the unburnt zone.

The hoppers were likewise almost exclusively confined to the burnt-over zone, and with numbers significantly higher in the $\frac{1}{4}$-mile band next to the contact line than in the band at $\frac{1}{4}$–$\frac{1}{2}$ mile from it. The numbers of hoppers in the unburnt

grass was significantly lower than might have been expected from the results of the egg-pod survey, suggesting that survival was lower there than under fresh grass following a dry-season fire. A subsidiary experiment, in which adult locusts were confined in cages placed on the lately burnt-over zone, the early-burnt and unburnt areas, respectively, suggested that, where there was no choice of oviposition site, the greatest number of surviving egg-pods occurred in the first zone, almost as many in the second and about half as many in the third.

During the incubation period, the soil under the unburnt grass was significantly colder, and tended to be moister, to moisten more slowly and to dry out less rapidly than that which had been burnt over. No significant correlation was found between incubation success in the burnt-over zone and total rainfall, mean recorded soil temperature or soil moisture.

It is concluded that, since these observations show that, for oviposition, adults of *N. fasciata* exhibit a very significant preference for ground that has been burnt over in the previous dry season, the burning of selected strips should lead to the concentration of oviposition and, consequently, of hoppers, thus making chemical control of the latter easier and cheaper.

There was some evidence, also, that when locusts could not move to bare ground, either oviposition or egg-pod survival (or both) were least successful where the grass cover was thickest.

References.

Backlund, H. O. (1956). Aspects and successions of some grassland vegetation in the Rukwa Valley, a permanent breeding area of the red locust.—*Oikos* suppl. 2, 132 pp.

Burnett, G. F. (1951). Field observations on the behaviour of the red locust (*Nomadacris septemfasciata* Serville) in the solitary phase.—*Anti-Locust Bull.* no. 8, 36 pp.

Chapman, R. F. (1958). Micro-climate in a locust habitat. (In prep.)

Faure, J. C. (1935). The life history of the red locust (*Nomadacris septemfasciata* (Serville)).—*Bull. Dep. Agric. S. Afr.* no. 144, 32 pp.

Michelmore, A. P. G. (1947). The habits and control of the red locust in outbreak areas and elsewhere.—*Bull. ent. Res.* **37** pp. 331–379.

Ramdas, L. A. & Draid, R. K. (1934). Soil temperatures.—*Curr. Sci.* **3** pp. 266–267.

Robertson, I. A. D. (1954). The numbers of eggs in pods of the red locust, *Nomadacris septemfasciata* (Serville) (Orth. Acrididae).—*Ent. mon. Mag.* **90** pp. 254–255.

Scheepers, C. C., Eyssell, B. J. & Gunn, D. L. (1958). Density distributions of hoppers of the red locust, *Nomadacris septemfasciata* (Serv.) (Orth. Acrid.), in relation to control by insecticides.—*Bull. ent. Res.* **49** pp. 467–478.

Scheepers, C. C. & Gunn, D. L. (1958). Enumerating populations of adults of the red locust, *Nomadacris septemfasciata* (Serville), in its outbreak areas in East and Central Africa.—*Bull. ent. Res.* **49** pp. 273–285.

Vesey-FitzGerald, D. (1955*a*). Applied ecology and indirect control.—*Rep. Dir. int. Red Locust Control Serv.* 1954 p. 31. (Unpublished.)

Vesey-FitzGerald, D. F. (1955*b*). The vegetation of the outbreak areas of the red locust (*Nomadacris septemfasciata* Serv.) in Tanganyika and Northern Rhodesia.—*Anti-Locust Bull.* no. 20, 31 pp.

VESEY-FITZGERALD, D. F. (1955*c*). Birds as predators of the Red Locust (*Nomadacris septemfasciata* Serv.).—*Ostrich* **26** pp. 128–133.

VESEY-FITZGERALD, D. F. (1957). The effect of fire protection on the vegetation. —*Rep. Dir. int. Red Locust Control Serv.* 1956 p. 38. (Unpublished.)

YATES, F. (1949). Sampling methods for censuses and surveys.—London, C. Griffin.

© Commonwealth Agricultural Bureaux, 1959.



FIG. 1. Contact between burnt and unburnt grass during the dry season, soon after burning.



FIG. 2. Experimental cages soon after the start of the wet season. The cage in the foreground is in grass burnt over during the previous wet season. That in the background is in grass unburnt for three years. This grassland starts immediately behind the nearer cage where herbs and bushes can be seen.



FIG. 1. Mowing strips for egg-pod search early in the wet season. The area in the foreground was burnt over in the dry season. The beacon has no connection with the experiment.



FIG. 2. Ploughing and searching for egg-pods early in the wet season in an area burnt over in the previous dry season.

DRIFT SPRAYING FOR VEGETATION BAITING.

By R. J. Courshee

National Institute of Agricultural Engineering.

By allowing a fine spray containing insecticide to drift downwind and land on surfaces across its path, spraying can be done quickly over large areas. The spray, moving nearly horizontally, is caused to land on vertical surfaces rather than horizontal ones, and by contaminating foliage in this manner, economies in insecticide expenditure may be made. This procedure has been used for baiting vegetation in the control of the desert locust, *Schistocerca gregaria* (Forsk.). The dispersal of the spray by the wind is here described quantitatively and the theoretical distribution compared with experimental results, in order to provide instructions for the use of drift-spraying techniques.

Drift Spraying.

In conventional applications of pesticides, spray is propelled from a nozzle towards the target that it is intended to cover, and some degree of control over this aim is achieved by selecting or positioning the nozzle. Drift dusting and drift spraying, on the other hand, are methods of application in which the dust or spray is released at a height above the ground and allowed to drift with the wind while it gradually sinks (Gunn & others, 1948; Courshee, 1950, 1951, 1952, 1955).

A number of factors will therefore affect the final destination of the material. In practice it is usually distributed across the first 100 metres downwind, largely, but not entirely, on the upwind side of vertical and exposed surfaces.

The two overall characteristics of the method are these. First, if a band 100 metres wide can be covered in each passage of the machine the design rate of work is 100 hectares an hour for each 10 km. per hour of the forward speed; this high speed may be of value for a number of purposes. Secondly, the application is controlled only partially by the machine and is influenced considerably by the wind.

Vegetation Baiting.

This is a name coined by R. J. V. Joyce (unpublished report of the Government Entomologist, 1953. Sudan Ministry of Agriculture) for the application of stomach poisons to natural vegetation for control of locusts. The term "spray baiting" has also been used in this sense (Sayer, 1959). It has more general significance for the use of any palatable pesticide that is a stomach toxicant and that is applied to the vegetation, natural or cultivated, likely to be consumed by a pest.

For our purposes, in application, the significant feature of vegetation baiting is that no attempt need be made to place the pesticide on to a pest, but that it should be placed on the vegetation or on that part of the vegetation that is going to be eaten.

Vegetation Baiting for Locusts.

A very widely used method of controlling locusts is to lay a poisoned bait made from bran where it may be found by locust hoppers. If the bait is taken by a suitable number of hoppers the method is usually effective and efficient in the use of insecticide (Rainey, 1957). But it is sometimes ineffective and it is a

cumbersome and costly method, and therefore inefficient from the broader viewpoint.

Joyce showed that by poisoning the natural food of the hoppers of *S. gregaria*, baiting could become more practicable. This he did at the time when insecticides and formulations suited both to vegetation baiting and to drift spraying became available. Previously, crops had been treated with insecticide for locust control and had thus been used as bait. It is only for the particular purpose of baiting certain types of desert vegetation with a drifting spray that the method here considered represents potentially a radical improvement. It is a method of applying pesticides that may be particularly suitable for the specified range of requirements and conditions of locust control. The economic value of the method can be inferred for any relevant circumstances providing the method can be shown first to be effective.

The toxicity of many insecticides to locusts is known; broadly, 99 per cent. lethal doses for insecticides in common use are of the order of 20μg. of insecticide per g. of insect (MacCuaig, 1958). Since the area of a fifth-instar hopper weighing 2 g. exposed to a cloud of spray drifting horizontally is between 1 and 5 sq. cm. (Wootten & Sawyer, 1954), the deposit density of insecticides needs to be between 40 and 8 μg. per sq. cm., if no shielding occurs, for contact killing to take place.

If the toxicant is palatable, cumulative and persistent, and if the locusts graze on contaminated foliage, a lethal dose will eventually be taken in. A locust hopper in the mid-fifth instar eats approximately 10 sq. cm. of foliage a day (Ellis & Ashall, 1957), and a lethal dose is thus accumulated in one day if the density of the insecticide deposit on the vegetation is 4 μg. per sq. cm. Lethal



Fig. 1.—The spray plume.

doses from less dense deposits would be acquired after a longer period of time if grazing continued in that spot.

The effective deposit density on the target might, therefore, be smaller for vegetation baiting than for contact spraying. Furthermore, the expenditure of pesticide necessary to attain a particular deposit density may be smaller on grass than on locusts, because of the configuration of the two targets. Against this possible economy must be set a lower probability, compared with contact spraying, that control will be obtained through vegetation baiting. The smaller deposit densities aimed at in vegetation baiting will cause only a small kill by contact action. Nevertheless, the method promises valuable economies in cost in comparison with conventional baiting programmes, and at least an equal degree of reliability. Moreover, the high rate of work of a drift sprayer is especially suited to the spraying of large bands or areas of ground, from, say, 50 metres square up to targets that are big enough to warrant attacking from an aeroplane. Finally, foliage contaminated with a persistent insecticide, such as dieldrin, appears to remain active for periods of several weeks.

By increasing the emission rate of insecticide and by making the spray coarser, the drift sprayer can also be used to apply spray directly to hoppers, rather than the vegetation, at a density of the order required for contact killing, whenever the target seems more suited to this control method. However, losses of spray on the ground between locusts will then increase.

The Distribution of a drifting Spray.

If a spray is released in the wind it quickly assumes the horizontal velocity V of the wind while it falls towards the ground at a speed f dependent upon the weight and size of the spray drops (fig. 1). The mean trajectory of the spray cloud is therefore along a line downwind inclined at an angle $\tan^{-1}(f/V)$ below the horizontal.

The spray is dispersed by the eddies in the wind to all sides of this mean path so that, in effect, the spray emitted from a point source forms a conical plume that drifts downwind. If the sprayer is moved across wind, the result is as though the spray had been emitted from a source in the form of a line, across the wind, as long as the run. Any diffusion of the spray horizontally at right angles to the wind will, on balance, cancel out and there is left only the diffusion in a vertical direction to influence the dispersion of the spray as it moves downwind.

This one-dimensional diffusion process permits a straightforward way of describing quantitatively the dispersion, providing a number of simplifying conditions are made. The more complex problem of the two-dimensional diffusion of a coarse aerosol has been considered by several people, most notably Bosanquet, Carey & Halton (1950).

Within the spray cloud, the concentration of airborne drops is a maximum on the axis and decreases with distance from the source and from the axis. Drops of a given size therefore land on the ground over a band downwind. The width of this band depends upon the height of the source and the degree of scatter of the spray away from the plume axis, and the point at which the axis of the plume strikes the ground depends upon its declination and upon the height of the source. In turn, the deposit density of the spray at points through this swathe (as the sprayed band is called) is controlled by these factors and by the amount of spray emitted per metre travelled across the wind. It is this deposit density on particular targets that is to be controlled at a desired level by selecting the conditions of spraying.

Assumptions made in calculating the Effects of Drift Spraying.

The axis of the plume of spray is known if the wind speed, terminal velocity of the droplets of spray and height of the source are known. The assumption is

made here that the wind speed is constant and equal to the speed at half the source height. In fact, the wind speed is greater above this height and less below it, but the error caused by the approximation is negligible in day-time, when the velocity varies according to only the seventh root of the height (Brunt, 1952).

A second assumption, that the spray consists of drops of one size only, may also be made, but is not necessary and for higher accuracy it could be avoided. Since the method of spraying requires the axis of the spray plume to be inclined at angles of between 3 and 9° below the horizontal, the spray used at moderate wind speed must be of the order of 100 μ in diameter for liquids of unit density. If a figure of, say, 80 μ corresponds to the mass median diameter of the spray spectrum, then the range of diameters containing 90 per cent. of the spray volume is likely to be 50–130 μ, depending upon the exact form of the distribution curve of drop size. Although it would be possible, for high accuracy, to consider the 130-μ drops, which will be falling relatively swiftly, separately from the 50-μ drops, falling relatively slowly, a valid simplification is made by assuming that all drops are 80 μ in diameter. A comparison of the deposit-density curves predicted for this range of drop sizes and for a spray containing only 80-μ drops is shown in fig. 2. This refers to day-time conditions, when the dispersion of the

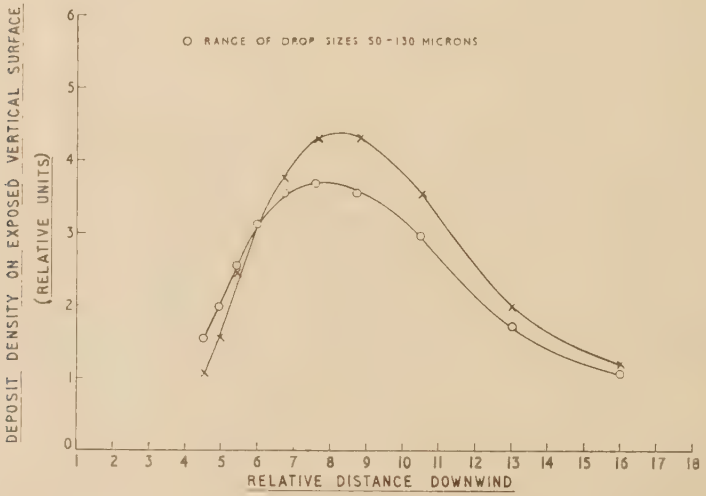


Fig. 2.—Theoretical deposit densities. Comparison of a spray with drop sizes ranging from 50 to 130 μ (circles) with one containing only 80-μ drops.

spray by eddies in the wind is powerful enough to mask the differences between the mean paths of the 50- and 130-μ drops.

We may thus regard the spray as homogeneous, but the approximation would become less valid if the drop spectrum were wider or the plume axis more steeply inclined, or if the spraying were done at night under inversion conditions, when the atmospheric scattering is less powerful.

Dispersion away from the Axis of the Plume.

At points off the axis of the plume, the concentration of spray decreases from the axial value. The concentration at a point, expressed as a fraction of the axial concentration at the same distance from the source, depends upon the angular

deviation of that point from the plume axis. Therefore, away from ground interference, the fraction of the spray cloud that is moving along a path inclined at a given angle to the plume axis is known. This dispersion in a vertical plane, measured over a period of the order of 30 minutes under gusty conditions, is shown in fig. 3.

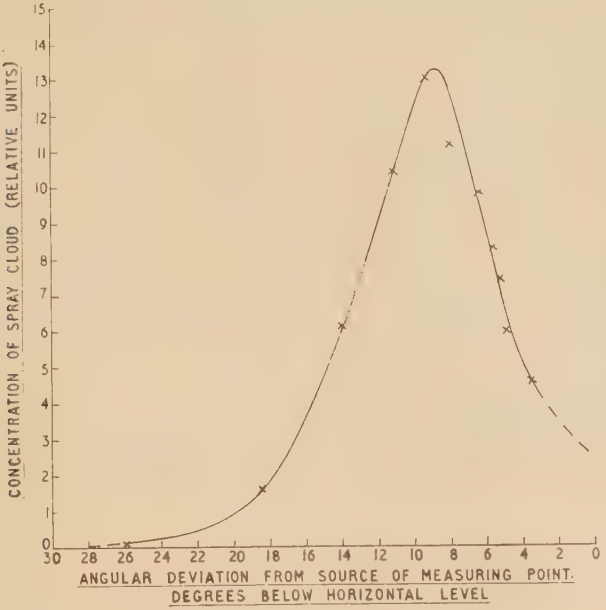


Fig. 3.—Experimental determination of the diffusion of a spray cloud in a vertical plane.

The quantity of spray contained within any narrow sector, say 1° wide, of the plume is distributed over that part of the target area covered by the sector. It is therefore possible to predict how the spray cloud will be scattered downwind, if we can predict the plume axis and the spread of the cloud away from the axis.

Near the ground, the distribution vertically about the axis will be asymmetric, both because the spray cloud is not reflected at the ground and because gustiness in the vertical direction tends to zero at ground level. The smaller dispersion downwards due to decreased gustiness probably does not occur until the spray is nearly located in the target area and it is unlikely to alter the general form of the results. It is important, however, in preventing the dilution that would otherwise occur as a result of spray reaching the ground and becoming unavailable to diffuse back towards the axis.

In effect, the ground does not materially alter the main distribution of the spray by altering gustiness, but it does provide an insulating layer of nearly stagnant air without which the cloud above it would rapidly become diluted. This dilution does in fact occur when a cloud drifts over a tall and dense ground crop. The greater the ability of the spray to penetrate into the vegetation and be trapped there, the less valid is the assumption that the angular dispersion remains constant for a trajectory inclined at a shallow angle. For steeper trajectories, interference from the ground cover becomes less and less important.

In practice, for the vegetation density shown in fig. 1, for example, corrections to the simple theory that follows do not appear to be needed in view of the correspondence of theoretical with experimental results.

Values of Angles of Dispersion.

Sutton (1949) quotes the width of the cloud emitted from a point source as 35 m. at 100 m. This is the time average for an interval longer than three minutes and corresponds to an included plume angle in a horizontal plane of $\pm 10°$. His other figures show $+6°$ in a vertical direction for the plume semi-angle for an emission from a source at ground level. Both figures are for adiabatic lapse conditions.

Because of the ground, the gustiness in a vertical direction is only 70 per cent. of the horizontal transverse gustiness at the height of two metres (Scrase, 1930). At 25 m., Best (1935) suggests that turbulence is isotropic.

Since diffusion is proportional to these eddy velocities, we can suggest that the angular width in a vertical direction of the plume formed several metres above the ground is less than the $\pm 10°$ given by Sutton for the angular width in a horizontal direction, but greater than the $+6°$ vertically that he gives for emission from a source very near the ground. A figure of $\pm 7°$ vertically has therefore been chosen to define the boundaries within which is contained 95 per cent. of the spray

The measured distribution of fig. 3 is wider than this, since it takes account of a longer period (30 minutes), and greater fluctuations in wind speed, than would be encountered in a spray run.

Angle of Inclination of the Plume.

From known terminal velocities of drops of unit density a graph may be made (fig. 4) to show the drop size necessary to give a required angle of fall for the

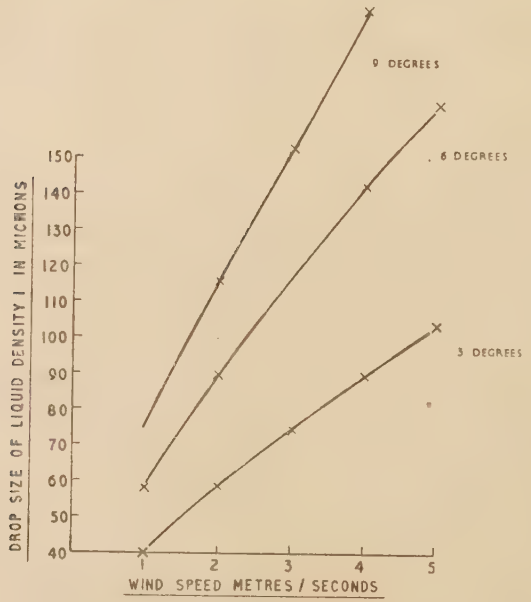


Fig. 4.—The relationship between wind speed and drop size for given angles of fall.

plume axis in different wind speeds. For a heterogeneous spray in the probable range of drop sizes of 50–150 μ, the falling speed of each size fraction is proportional to a power between 1 and 2 of the diameter of the drops in that fraction. Probably the mean diameter of the spectrum that will best characterise the behaviour of the spray as a whole is that corresponding to the mode of the frequency distribution of spray volume by drop size. This is usually less than the mass median diameter, and the surface-volume mean diameter * of the spray appears to give results that conform with this theory.

The form of the distribution graph and its position downwind are in accord with the theory if the surface-volume mean diameter is used to predict the trajectory but, as shown in fig. 5, some improvement is needed to make the agreement

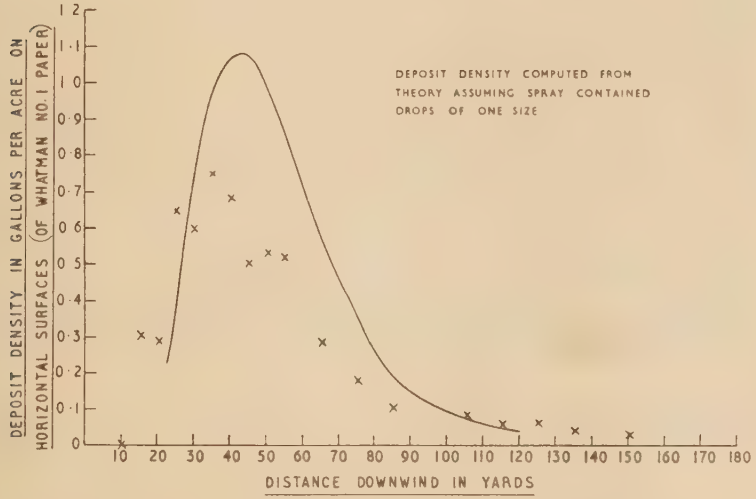


Fig. 5.—Comparison of theoretical and experimental deposit densities. Measured deposit density from Coursbee (1952). Full line shows the computed deposit density.

accurately quantitative. Better qualitative agreement is obtained with a spray of drops of one size (fig. 6).

Jarman's results (1958) on the receptiveness of various surfaces to a cloud of spray falling in this fashion suggests that some refinement of technique is required before considering amendments to the theory.

Conditions of Inversion in the Atmosphere.

Under inversion conditions, such as may occur after dawn but before sunshine warms the ground, the wind is more nearly streamlined. The scattering of the

---

*Surface-volume mean diameter $= \dfrac{\Sigma_0^{D_m} N_D D^3}{\Sigma_0^{D_m} N_D D^2}$,

where D_m = maximum drop diameter, and N_D = no. of drops in class interval with mean diameter D.

spray cloud away from the mean path is then less pronounced, so that the deposit tends to be concentrated closer to the axis. Moreover, trajectories with slightly different angles of fall then overlap to a smaller extent, so that the assumption that the spray consists of drops of one size is less accurate.

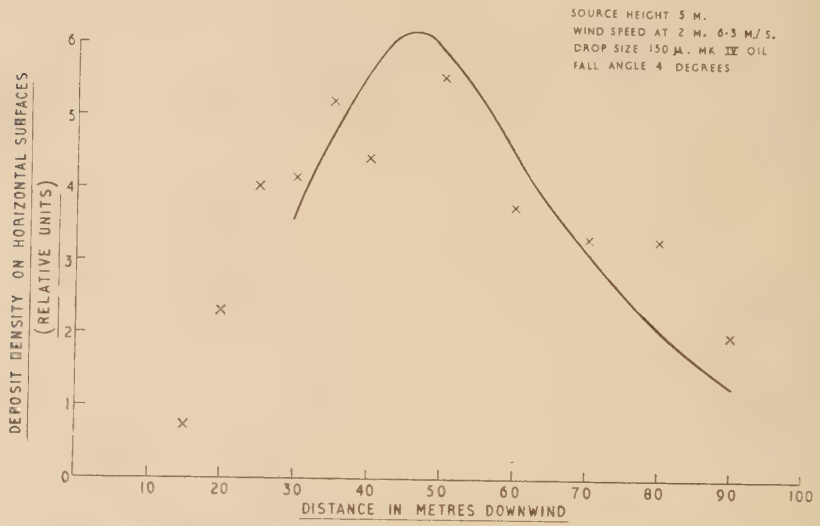


Fig. 6.—Exp[illegible] spray-deposit densities on horizontal surfaces. Dispersion of drops of [illegible] Full line shows theoretical dispersion for these conditions.

The deposit curves from vertical surfaces arising from applications when the angle of dispersion is 3·5° are shown in fig. 7, and should be compared with those for an angle of dispersion of the normal ±7°, given in fig. 10.**

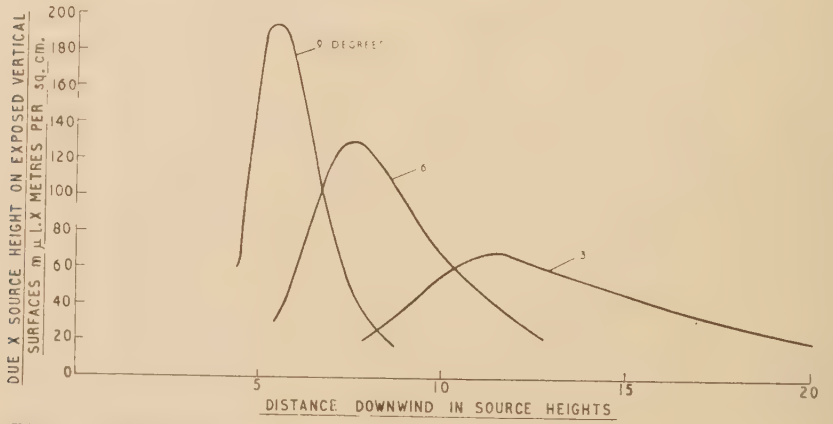


Fig. 7.—Theoretical deposit densities on vertical exposed surfaces. Comparison of several angles of fall when the plume diffusion angle is ± 3·5 degrees.

** For an explanation of the terms and units of measurement used in figs. 7–11, see the section headed "Worked Examples" on p. 365.

Evaporation.

Using such a fine spray as is necessary, rates of evaporation can be high, since both the convective and radiation heat transfer coefficients (calories per sq. cm. for unit mass of spray) are inversely proportional to drop size (Perry, 1955). In early trials, domestic paraffin was used and no spray was recovered at all. Jarman's more complete results (Hill & Jarman, 1958) show how evaporation increases with distance downwind. His measurements show only a few instances of complete evaporation, but he was using a spray that was both relatively coarse and contained a non-volatile fraction.

Experiments in the Sudan to test drift spraying and vegetation baiting were initially unsuccessful, as very low deposit densities were obtained using conventional spray formulations. The use of solutions of insecticide in a proprietary oil* prevented the evaporation and removed this source of variation in the deposit densities obtained. (Courshee, R. J., Amsden, R. C. & Morris H. J. Unpublished report of the Government Entomologist, 1956. Sudan Ministry of Agriculture.)

Spray Deposits.

The foregoing sections enable the fraction of the spray contained within each vertical one-degree-wide sector of the wedge-shaped cloud to be known. Equally, if the plume axis and the source height are known, the bands of ground covered by these one-degree-wide sectors are determined.

The inclination of the plume axis to the horizontal must be chosen, but once this is done, if distances downwind are indicated in terms of source heights, a single graph defines the deposit density for all source heights (fig. 8) for an emission of one millilitre per metre travelled across the wir

The interest for vegetation baiting lies mainly in the s on the nearly vertical stems of grass, and probably on the younger tips . than the woody

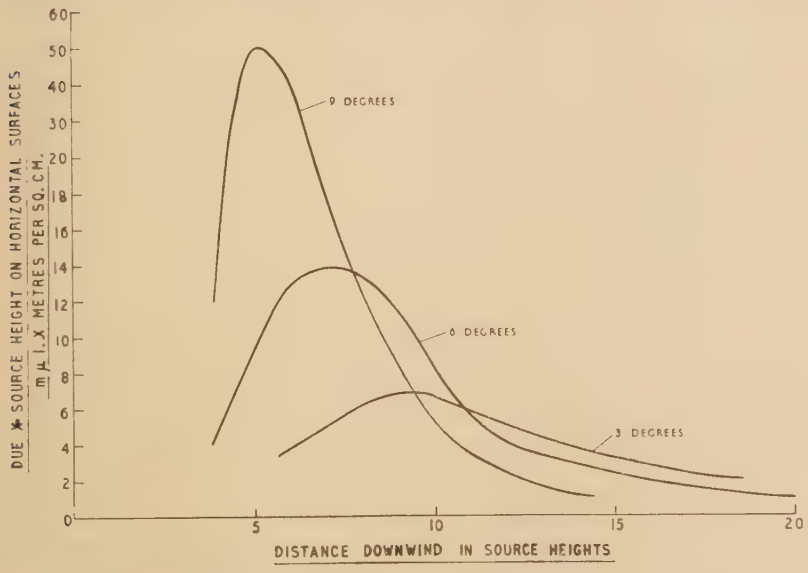


Fig. 8.—Deposit densities on horizontal surfaces. Comparison of several angles of fall when the plume diffusion angle is ±7 degrees.

* Dutrex 3, marketed by Messrs. Shell Chemical Co., Ltd.

base. If the vegetation is sparse, then the density we need to know is that on nearly vertical surfaces fully exposed to the spray.

By the geometry of similar triangles, and assuming that the spray is coarse enough for its impaction efficiency to be high, the deposit density on a vertical surface should be n times that on a horizontal one, where n is the distance downwind (in source heights) of the position where the samples are taken. An

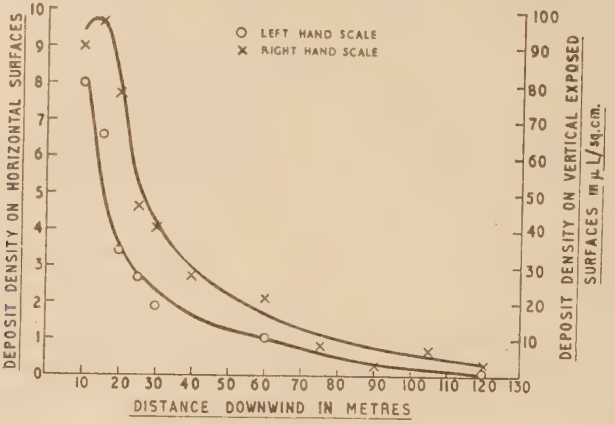


Fig. 9.—Experimental comparison of deposits on vertical and horizontal targets.

experimental comparison between deposits on vertical and horizontal surfaces is shown in fig. 9.

The deposit densities on vertical surfaces for several angles of inclination of the plume axis are shown in fig. 10, the distance downwind being measured in

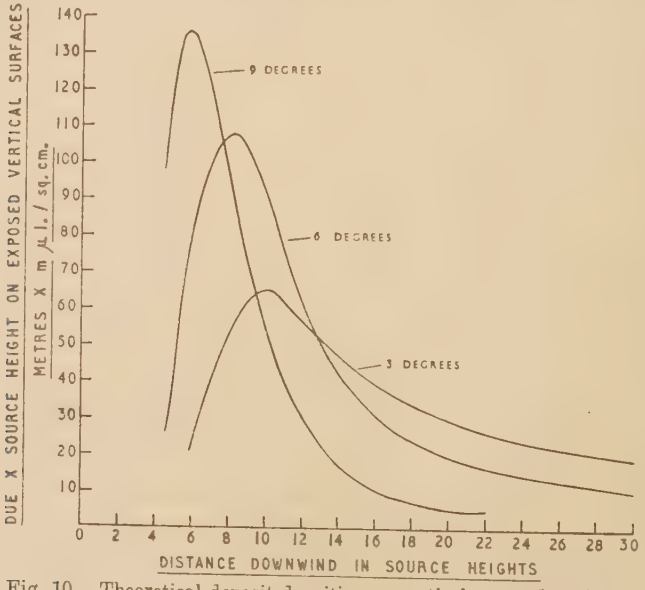


Fig. 10.—Theoretical deposit densities on vertical exposed surfaces. Comparison of several angles of fall when the plume diffusion angle is ±7 degrees.

terms of the height of the source. A theoretical comparison, fig. 11, is also given for the deposits on vertical and horizontal surfaces and this may be contrasted with the experimental comparison of fig. 9.

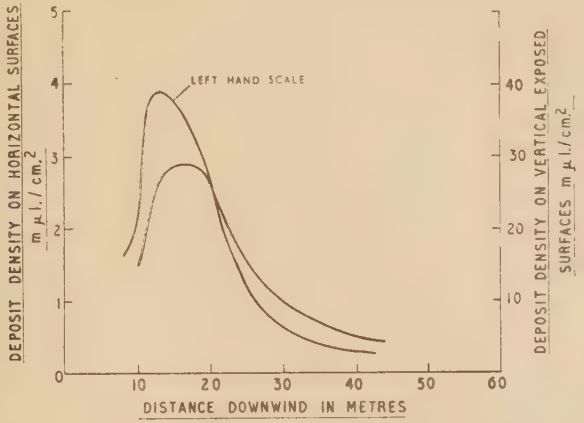


Fig. 11.—Theoretical comparison of deposits on vertical and horizontal targets.

Worked Examples.

The usefulness of the theory is that it facilitates a fairly quick prediction of the result of spraying, or the selection of spray conditions for a required deposit. Either of these operations can be effected by using the graphs showing the values of the quantity DUE, that is, the deposit density for unit emission, at different distances downwind for several angles of fall of the spray, either on horizontal surfaces (fig. 8) or vertical surfaces (fig. 10). The angle of fall can be selected or determined for given wind speeds and spray-drop size from fig. 4.

The deposit is related to the strength of the source and, in the graphs shown in figs. 7–11, a constant source strength has been used of one millilitre per metre travelled across the wind. Distances are presented in terms of the height of the source; the deposit from a high source will occur further downwind than will that from a lower one, and the given amount of spray will be spread more thinly over a wider area. The deposit densities shown in the graphs are related to a source one metre high and the units of the ordinates are micromillilitres (mμl.) per sq. cm. × source height in metres.

Example 1.

To predict the deposit curves, let the operating conditions be: source height, 2 m.; wind speed at 1 m. height, 1·5 m. per sec.; source strength, 5·5 ml. per metre; drop size, 80 μ; specific gravity of liquid, 1 g. per ml.

From fig. 4 it is seen that the plume axis will lie approximately 6° below the horizontal. Then from fig. 8 the deposits on horizontal surfaces can be predicted for a source 1 m. high emitting 1 ml./metre.

For a source 2 m. high, the distances in metres are twice the distance in source heights and the deposit densities half as great as those given in fig. 8. Since, however, the source strength is 5·5 times the unit source, the deposit densities are finally $\frac{5{\cdot}5}{2}$ times as great as those given in fig. 8.

A corresponding result could be obtained from fig. 10 for the deposits on vertical surfaces, or these can be deduced from the deposits on horizontal surfaces

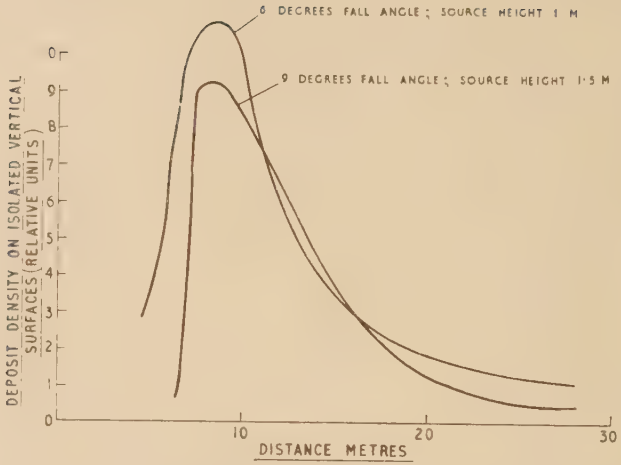


Fig. 12.—Theoretical spray-deposit densities on vertical exposed surfaces. Example of changing source height to compensate for a change in angle of fall.

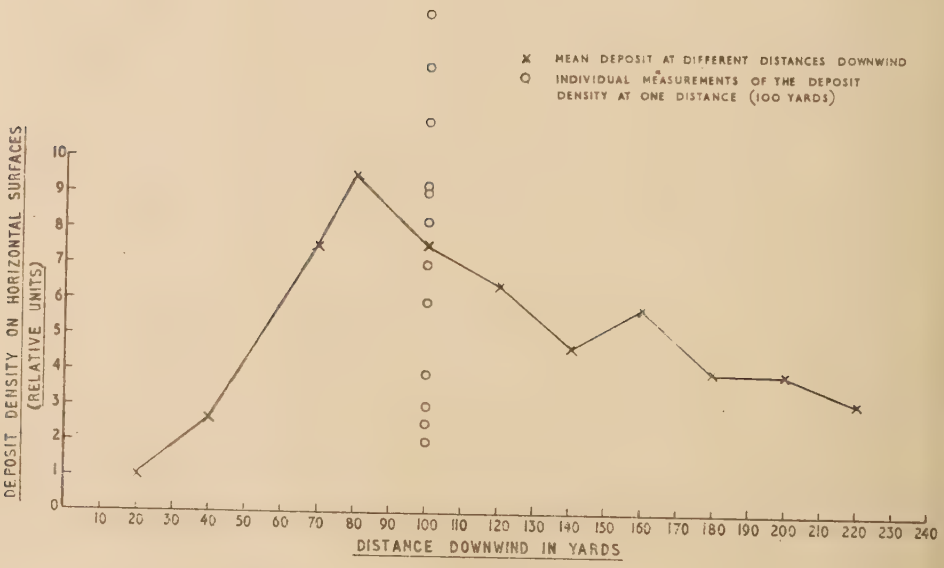


Fig. 13.—Experimental spray-deposit densities. Example showing the variability of the deposit along a line parallel to the source, from Courshee (1952).

by multiplying each of them by the corresponding distance expressed as a multiple of the source height.

Example 2.

For a required deposit-density curve: to predict the necessary operating conditions.

The shape of the distribution curve cannot easily be influenced; it is its position and the numerical value of the density at one point on it that can be controlled.

Generally, it would seem that a fall angle in excess of 6° is desirable to preclude a loss from spray rising above the horizontal level. If 6° is chosen, then the drop size to suit the wind speed occurring can be chosen. The swathe width can then be obtained by altering the source height and, if necessary, the strength of emission. The deposit-density curve rises to a peak and then falls again, and so the swathe width may be defined as the band throughout which the deposit density is greater than any specified level.

If a choice of 6° for the fall angle is made, then a mechanism for selecting drop size is desirable, or it will be necessary to restrict operations to a range of wind speeds allowing the fall angle to lie in the range 5–7°, for example. It is possible, however, to achieve the effect of a given fall angle by using a greater angle and raising the source height, as shown in fig. 12, which shows how a change in fall angle from 6° to 9° can be compensated by raising the source from 1 m. to 1·5 m. A lower source and a shallower trajectory than 6° is less desirable because of the loss that may occur of spray beyond the target area.

The values of DUE predicted by this method are the average values at given distances downwind and considerable variation along a line parallel to the spray run is encountered in practice (fig. 13) and can best be overcome, should this be necessary, by decreasing the spacing between consecutive spray runs. Since the variability is similar to that found in more conventional spray applications, it possibly does not affect the efficiency of vegetation baiting to an important extent.

Summary.

The term drift spraying denotes a method of applying an insecticidal spray whereby it is released at a height above the ground and allowed to drift with the wind while it gradually sinks; if the source of emission is moved in a line across the direction of the wind, insecticide will be deposited at a distance downwind of that line. The method has been used for vegetation baiting, a term meaning the application of stomach poisons to natural vegetation for control of locusts; this may be more economical than the application of contact insecticides to the insect itself.

Spray particles emitted from a point source have a mean trajectory downwind inclined to the horizontal at an angle of $\tan^{-1}(f/V)$, where f is their terminal velocity and V the windspeed, and they are dispersed by wind eddies to all sides of this mean axis so as to form a conical plume; if the source is moved across the wind, horizontal dispersion normal to the wind tends to cancel out and only the vertical component of the dispersion need be considered. The concentration of spray drops is a maximum on the plume axis and decreases with distance from it. The spray cloud from such a source thus occupies a wedge-shaped space as it drifts downwind, and it reaches the ground over a band whose width depends on the height of the source and the degree of dispersion. The point at which the plume axis strikes the ground is determined by its declination and by the height of the source; the density of the spray deposit, whose overall value is determined by width of the band sprayed and by the quantity of spray emitted from the source per unit distance travelled across wind, is a maximum upwind from this point and diminishes more steeply towards the upwind edge of the band than towards the downwind one.

Large drops will fall faster and hence be deposited nearer the line of emission than will small drops, but in practice, in day-time, the effects of dispersion by wind eddy tend to exceed and mask those due to the range of drop size and it is thus a valid simplification to consider the spray cloud as composed of drops all of one size. The behaviour of heterogeneous sprays is best characterised by the assumption that all drops are of a diameter equal to the surface-volume mean diameter. At moderate wind speeds, the drop diameter used should be of the order of 100μ, and an oil of low vapour pressure is needed if the tendency of such small drops to evaporate before reaching the target is to be prevented.

The angle of dispersion probably depends on the degree of wind turbulence. Experimental measurements of the concentration of drops within a spray plume, relative to that on the axis and at different angular deviations from the latter, enable the fraction within each sector to be known, and suggest that for normal atmospheric conditions, when the lapse rate is adiabatic, 95 per cent. of the spray is contained within $\pm 7°$ of the plume axis in the vertical plane.

The calculated densities of deposits on a horizontal surface at varying distances downwind, related to a source whose height and rate of emission are unity, are shown as graphs for different values of the declination of the plume axis (predictable from the wind speed and drop size) and are compared with experimental measurements. Using these data, the conditions that will afford any desired deposit density can be selected. Since the interest of drift spraying for locust control lies mainly in the deposits on the nearly vertical stems of grass, similar data are given for values of the deposit density on an exposed vertical surface, which can be shown to be n times that on a horizontal one at the same distance downwind, when the latter is expressed as a multiple, n, of the source height.

Acknowledgements.

The work was initiated and encouraged by R. J. V. Joyce, then the Chief Entomologist, Ministry of Agriculture, Sudan. The experimental part was done with the help of R. W. Valentine of the National Institute of Agricultural Engineering and R. C. Amsden of Messrs. Fison's Pest Control, Ltd. The photograph used for fig. 1 is reproduced by courtesy of Dr. D. L. Gunn.

References.

Best, A. C. (1935). Transfer of heat and momentum in the lowest layers of the atmosphere.—*Geophys. Mem. Lond.* no. 65, 66 pp.

Bosanquet, C. H., Carey, W. F. & Halton, E. M. (1950). Dust deposition from chimney stacks.—*Proc. Inst. mech. Engrs* **162** pp. 355–360.

Brunt, L. D. (1952). Physical and dynamical meteorology.—London, Cambridge Univ. Pr.

Courshee, R. J. (1950). "Innominate" locust sprayer trials.—*Tech. Memor. nat. Inst. agric. Engng* no. 38.

Courshee, R. J. (1951). "Airflow" locust sprayer trials.—*Tech. Memor. nat. Inst. agric. Engng* no. 46.

Courshee, R. J. (1952). Drift spraying for locust control with ground machines.—*Tech. Memor. nat. Inst. agric. Engng* no. 50.

Courshee, R. J. (1955). Further trials of drift spraying for locust control.—*Dep. Note nat. Inst. agric. Engng* no. 54.

Ellis, P. E. & Ashall, C. (1957). Field studies on diurnal behaviour, movement and aggregation in the desert locust (*Schistocerca gregaria* Forskål).—*Anti-Locust Bull.* no. 25, 94 pp.

Gunn, D. L. & others (1948). Locust control by aircraft in Tanganyika.—153 pp. London, Anti-Locust Res. Cent.; Pretoria, Locust Control Res. Sect., Dep. Agric. S. Afr.

Hill, R. F. & Jarman, R. T. (1958). The performance of some rotary sprayers.—*J. agric. Engng Res.* **3** pp. 205–213.

Jarman, R. T. (1958). The deposition of wind-borne oil droplets on various horizontal surfaces.—*J. agric. Engng Res.* **3** p. 131.

MacCuaig, R. D. (1958). The toxicity of insecticides to adult locusts.—*J. Sci. Fd Agric.* **9** pp. 330–342.

Perry, J. E. *Ed.* (1955). Chemical engineers' handbook.—New York, McGraw Hill.

Rainey, R. C. (1957). Methods of insecticide application against the desert locust.—*Plant Prot. Conf. 1956* pp. 283–287.

Sayer, H. J. (1959). An ultra-low-volume spraying technique for the control of the Desert Locust, *Schistocerca gregaria* (Forsk.).—*Bull. ent. Res.* **50** pp. 371–386.

Sayer, H. J. & Rainey, R. C. (1958). An exhaust-nozzle sprayer for ultra-low-volume application of persistent insecticide in locust control.—[4] pp. London, Anti-Locust Res. Cent.

Scrase, F. J. (1930). Some characteristics of eddy motion in the atmosphere.—*Geophys. Mem., Lond.* no. 52, 16 pp.

Sutton, O. G. (1949). Atmospheric turbulence.—London, Methuen.

Wootten, N. W. & Sawyer, K. F. (1954). The pick-up of spray droplets by flying locusts.—*Bull. ent. Res.* **45** pp. 177–197.

Appendix.

Experimental Methods.

The spray emitted during a run of known length is measured by the fall in liquid level in a calibrated reservoir. This reservoir can be recharged or the spray applied directly from the main tank by changing the valves of the apparatus shown in fig. 14.

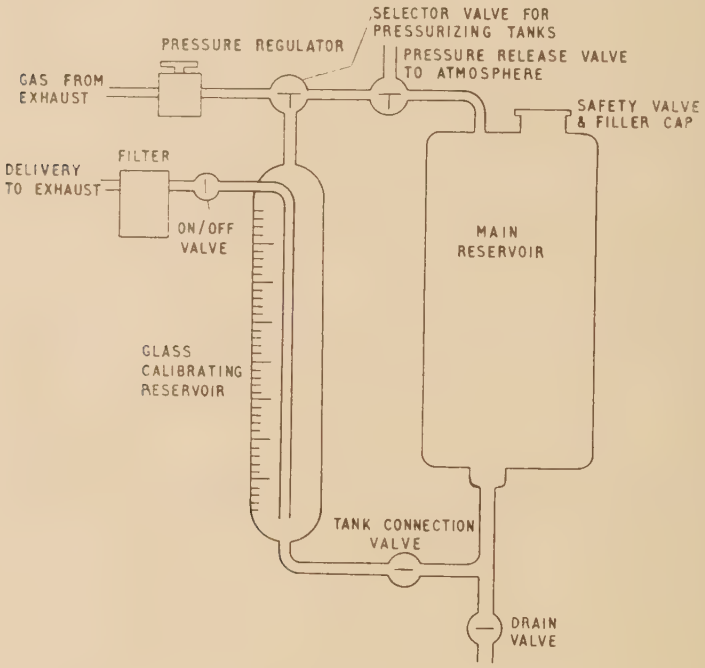


Fig. 14.—Measurement of output of liquid from sprayer.

Under the pressure of the restricted exhaust gases of the motor vehicle carrying the sprayer, the spray is fed to an air-blast nozzle through which the exhaust gas escapes and atomises the spray liquid. This is a particularly simple form of machine for this work (Sayer & Rainey, 1958).

To detect the spray on a target, a tracer is added and measured by conventional chemical or photometric techniques. The ground targets used were glass slides laid on horizontal wooden blocks 3 cm. thick, and they were unshielded by vegetation. To simulate vertical stems of grass, short lengths of glass tubing 5 mm. in diameter were placed on vertical wires 30 cm. above the ground. A cylindrical receiver provides a convenient way of avoiding the change in deposition that would occur on a flat vertical surface whenever the orientation of the wind changed.

© Commonwealth Agricultural Bureaux, 1959.

AN ULTRA-LOW-VOLUME SPRAYING TECHNIQUE FOR THE CONTROL OF THE DESERT LOCUST, *SCHISTOCERCA GREGARIA* (FORSK.).

By H. J. Sayer

Desert Locust Survey, East Africa High Commission.

(Plates VII & VIII.)

The method of control of the desert locust, *Schistocerca gregaria* (Forsk.), that is at present most widely used is "baiting", in which a suitably attractive edible material, usually wheat bran, is mixed with a relatively small amount (0·1 per cent.) of toxicant (γ BHC or, sometimes, aldrin) and spread on the ground among bands of hoppers. Control operations against a large-scale and potentially dangerous infestation of hoppers may utilise thousands of tons of bait, which have often to be transported over many hundreds of miles of barren country with few or inadequate roads or tracks, and finally distributed by hand. The problem of control by baiting is, therefore, mainly one of transportation of bait and the organisation of the large labour force required to mix, handle and spread it. Clearly, any control technique that can substantially reduce the transportation and labour requirements stands a good chance of reducing the overall cost and the administrative burden of locust control.

Bait contains 99·9 per cent. non-toxic edible materials, but it exerts no attraction to hoppers at a distance, and it has to compete with their normal food. The latter is usually the fresh green growth of vegetation resulting from recent rains. Locust eggs can develop only in moist sand or soil, and the necessary moisture, usually the result of recent rains, also causes the germination of seeds or the revival of desert vegetation, so that by the time the hoppers emerge there is a fresh new growth on which the marching bands of hoppers live. If an insecticide can be easily and satisfactorily applied to this vegetation, the edible part of bait need not be transported. This procedure has been termed "spray baiting" by Joyce (Joyce, R. J. V., Morris, H. J. & Amsden, R. C. The control of hoppers of *Schistocerca gregaria* Forsk. by low volume drift spraying of insecticide concentrates. Unpublished report. Sudan Ministry Agriculture, 1955). The term "vegetation baiting" has also been used in this sense (Courshee, 1959). In such a plan, the vegetation itself is used as the carrier for the poison, thus affording considerable economy of transportation costs.

Development of Sprayer and Spraying Technique.

During 1951 and 1952, attempts to spray swarms of the desert locust by the ground machines then available in the Desert Locust Control organisation showed that commercial sprayers, large and expensive and correspondingly few in number, had little chance of making contact with mobile swarms, moving 30–70 miles per day over often trackless bush country. Moreover, much difficulty was experienced in maintaining the machines with their own petrol engines in working order hundreds of miles from workshop facilities. The control organisation uses Land-Rovers and is equipped to maintain them, and it was thought that if a simple spraying device could be designed for the Land-Rover, and each field officer supplied with one, then the chances of intercepting swarms would be greatly enhanced. Consequently, a sprayer was designed in which atomisation was effected by a restricted exhaust orifice surrounding a jet of liquid, the back

pressure caused by the restriction being used to feed the liquid from a drum to the jet. This design was first used in 1953 with DNC to spray a settled swarm in bush country in the Northern Frontier Province of Kenya and it was shown that spraying in the early morning caused flushing of the locusts so that they flew at very high densities in the plume of spray from the nozzle; this gave good kills per gallon of insecticide, by contact poisoning, although on a scale that was very small in relation to the numbers of locusts in swarms, which may amount to hundreds of millions per square mile.

The original design was presented at a meeting of the Food and Agriculture Organisation's Technical Advisory Committee on Desert Locust Control (3rd meeting. Committee paper no. 8. Item 11. FAO/53/4/2807). The machine, and the technique of its use, termed drift spraying (Courshee, 1959), have been successfully used in Morocco (Lhéritier, 1955), against grasshoppers in South Australia (Osborne, 1956) and for the control of flea-beetle in the Sudan (Toms & Goodman, 1957), and further examples of their use against *S. gregaria* are given here.

In July 1953, Thompson, spraying water-miscible Acrodel (an 11 per cent. γ BHC concentrate) at dilutions in water of 1 in 5 and 1 in 28, destroyed small bands of second- and third-instar hoppers of *Schistocerca* (Thompson, B. C. Unpublished report on exhaust sprayer trials in Eritrea, 1953). He used the nozzle at 30° above the horizontal and applied 1¼ to 2 gal. of the diluted mixture per acre. Later trials with Acrodel against third- and fourth-instar hoppers carried out in the Northern Frontier Province of Kenya were, however, disappointing, in that direct applications of similar emulsions to hoppers gave poor kills. No attempt was made to assess any stomach-poison effect.

In April–May 1954, an exhaust-nozzle sprayer was used by Milnes and Tompkins ([Shell Petroleum Company, 1954] Fb. 15) with water dilutions of dieldrin and aldrin against egg-fields and against fourth- and fifth-instar hoppers. The technique adopted was to spray a 1 in 25 dilution in water of Dieldrex 15 (18 per cent. dieldrin), applying about one gallon of the mixture per acre on a closed lattice 45-yd. square in one case and 10-yd. square in another. With this technique they obtained 14 days' persistence on the egg-field site and in other operations they noted an effective persistence of four days against fourth- and fifth-instar hoppers.

Joyce, Morris & Amsden (see p. 371) used a modified sprayer with DNC, γ BHC and aldrin against fifth-instar hoppers. They obtained only 30 per cent. and 7 per cent. kills with the first two but demonstrated that with an output of 0·08 gal. Aldrex (40 per cent. aldrin concentrate) per 100 metres run, or an estimated mean dosage of 0·0025 gal. of concentrate (9·7 g. aldrin) per acre, a 99 per cent. control was obtainable. The aldrin acted mainly as a stomach poison, and they pointed out that although the technique had a lower efficiency than the normal baiting technique, this lower efficiency could be tolerated in view of the enormous saving in the cost of haulage of the bait carrier.

Development work on the exhaust sprayer was undertaken by Courshee (1955) at the National Institute of Agricultural Engineering and he showed that tractor vapourising oil was too volatile for recovery and therefore unsuitable for drift spraying. He pointed out that it was desirable to have a fine spray for recovery on vertical surfaces and suggested that it was probably necessary to pay attention to the design and finish of the nozzle in order to avoid producing the wasteful large drops.

Morris, using dilutions of emulsifiable aldrin in kerosene and diesel fuel in the Sudan, failed to recover any spray or obtain any kill beyond 10–20 m. from the sprayer (Morris, H. J. Spraying aldrin and dieldrin concentrate with a Land-Rover exhaust-sprayer against Desert Locust hoppers. Unpublished report. Sudan Ministry of Agriculture, 1955). He showed, however, that 5 per cent.

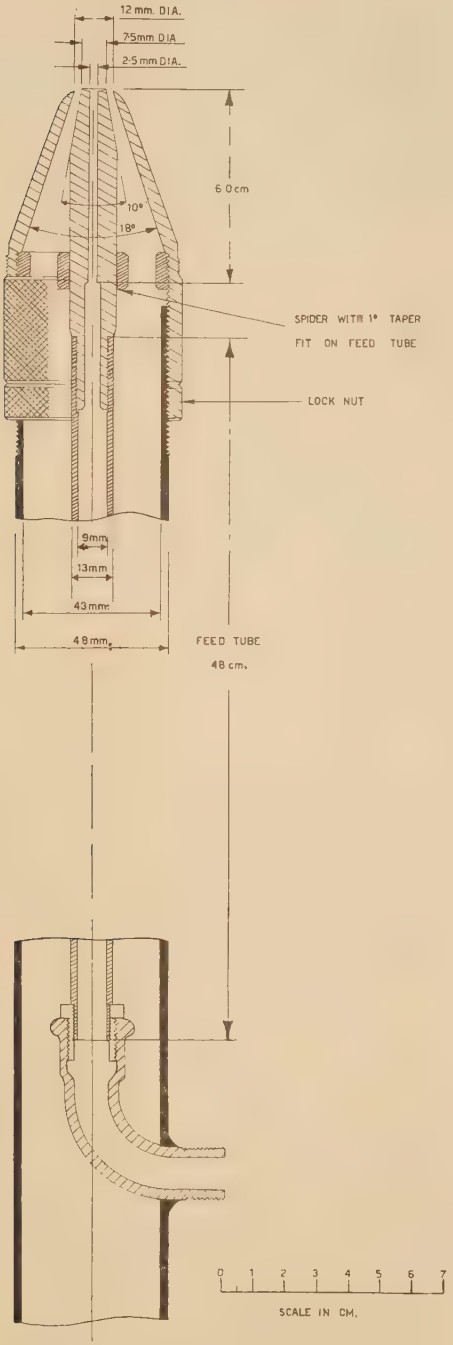


Fig. 1.—Exhaust nozzle designed to be self-centring.

dieldrin dissolved in a mixture of motor-car lubricating oil and diesel oil gave satisfactory kills, but pointed out that the mixture was unsatisfactory as regards both viscosity and the solubility of dieldrin.

Following these results, a programme of further work was undertaken at Asmara, Ethiopia, in 1956 to study the technique of producing a spray deposit on typical desert vegetation, under the temperature and other conditions experienced in the desert, which would be toxic to hoppers marching amongst and feeding on that vegetation, and to re-design the sprayer to eliminate a number of defects that had shown up in the original model.

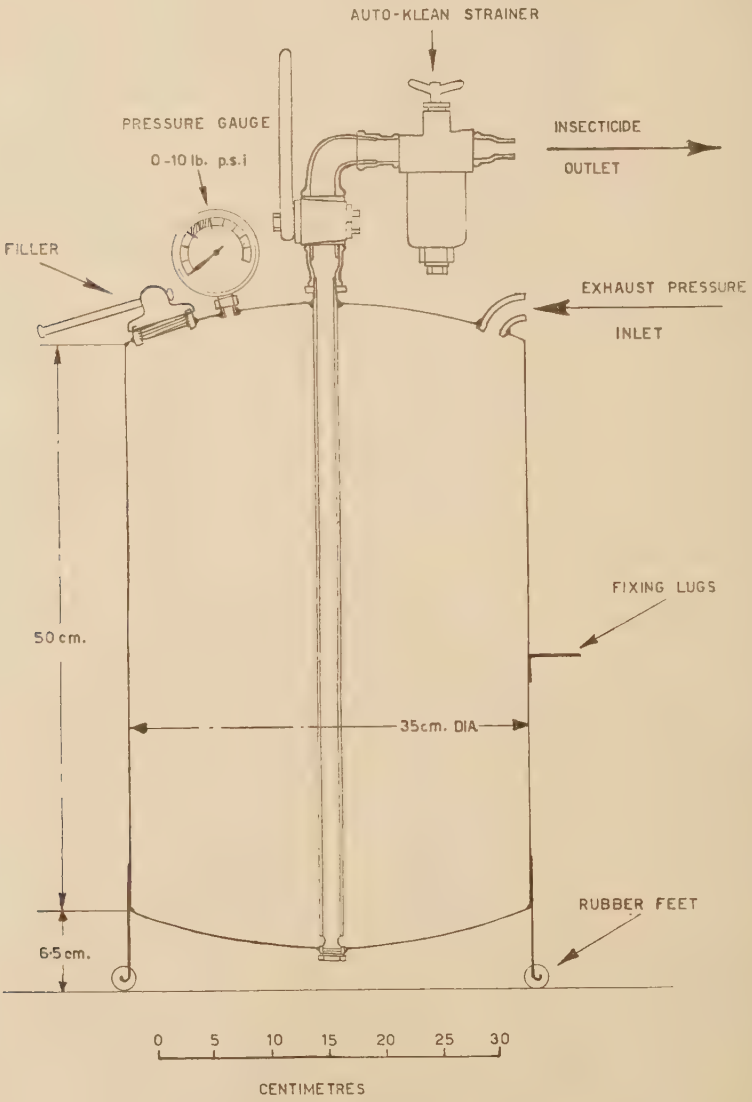


Fig. 2.—Ten-gallon insecticide tank.

The original machine was accordingly re-designed, to give the finest possible spray compatible with a reasonable emission rate. The nozzle was made conical, to give improved entrainment of the surrounding air, and special attention was given to the means of centring the liquid jet in respect of the conical cap. This centring was first attained by making the jet adjustable in two dimensions by means of screws on a supporting feed tube; this design was successfully used in the early trials and is described and illustrated in a leaflet issued by the Anti-Locust Research Centre, London (Sayer & Rainey, 1958). A simpler jet mounting was finally developed which is largely self-centring, and details of this modified design and its spray tank are given in figs. 1 and 2. The insecticide drum in its final form consisted of a pressure-resistant. mild-steel drum fitted with a

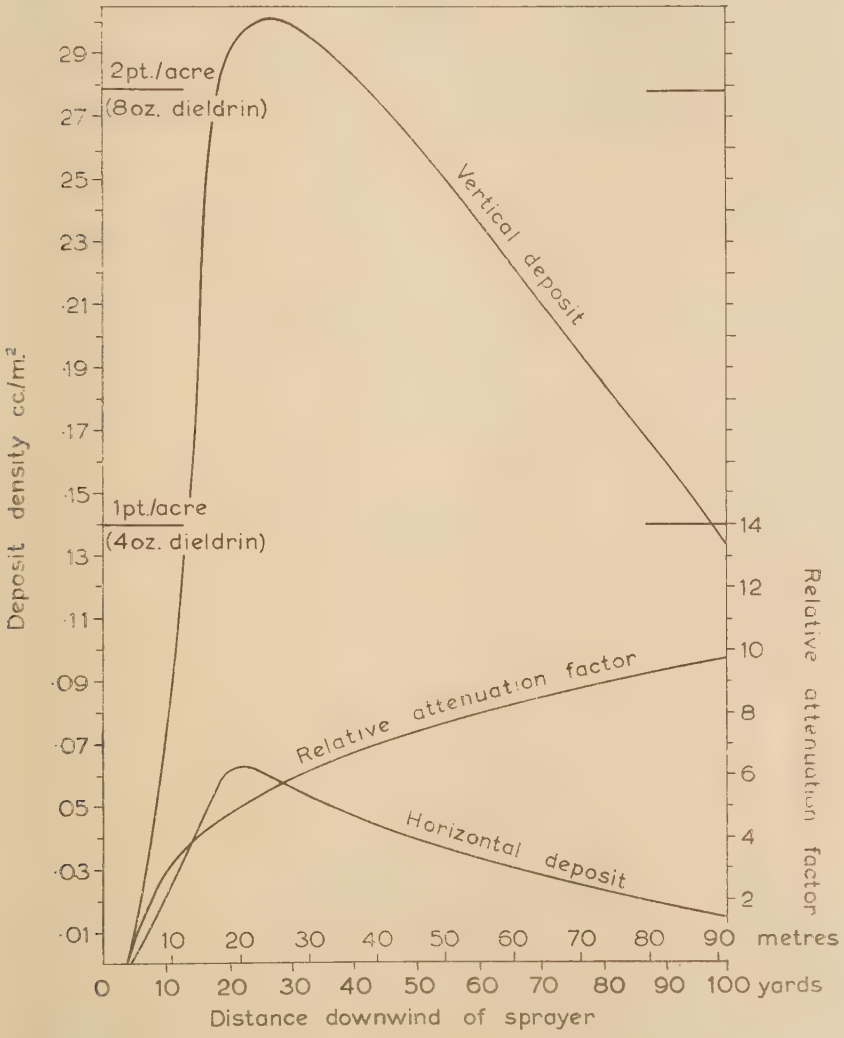


Fig. 3.—Typical deposit recovery curves, showing horizontal deposit, vertical deposit and relative attenuation factor.

manometer, stopcock and Auto-Klean filter; the feed tube was a braided petrol hose and the exhaust pressure tube a flexible metal heat-proof tube. A safety valve made from a car valve fitted to a T-union was incorporated in the nozzle and, by means of a light spring, set to release at 7 lb. per sq. in. This valve is necessary in order to avoid any accidental increase of back pressure above 7 lb. p.s.i., which might damage the exhaust valves of the car engine. A typical spray-deposit trial, in which 7 cc. of spray was emitted per metre of run cross-wind, showed that the mass median diameter (m.m.d.) of the recovered spray over 212 metres downwind was 69 μ, and that 57 per cent. of the emitted spray was recovered over this distance (see figs. 3 and 4). The m.m.d. of the total spray (that is, including the proportion not recovered within the sampled area) may be presumed to be much lower than this.

Pearson [1958] has shown that the LD90 of dieldrin for fifth-instar hoppers of the desert locust is about 10 μg., and Ellis & Ashall (1957) found that such hoppers, caged in the field, ate a maximum of the order of 10 sq. cm. of leaf surface per day. These figures suggest that a deposit density of 10 μg. per 10 sq. cm., or 0·01 g. of dieldrin per sq. metre of vegetation is necessary in order to control the most difficult instar, the fifth.

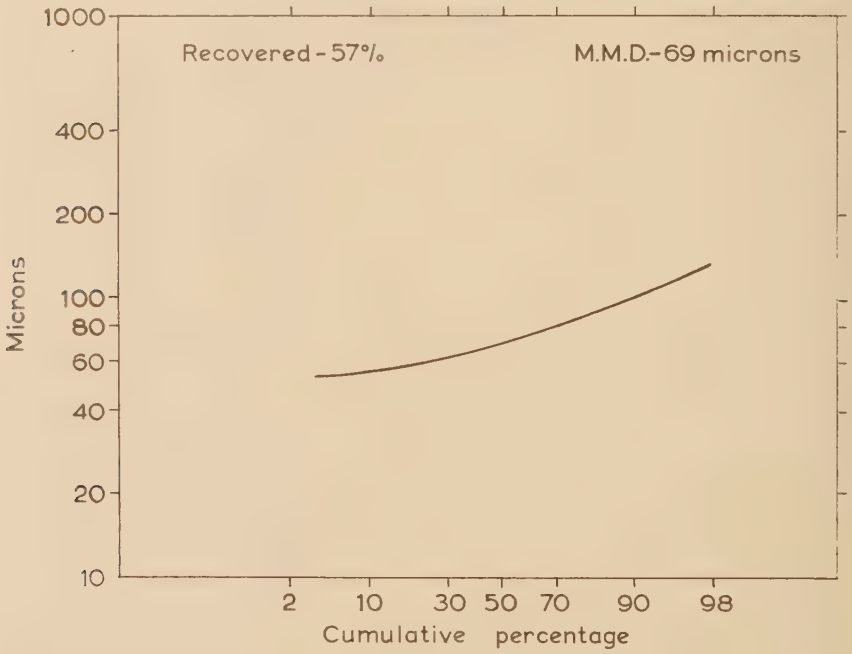


Fig. 4.—Drop spectrum of the spray produced by exhaust-nozzle sprayer. Ordinates represent drop diameter in microns.

Fig. 3 shows that horizontal ground deposit produced by drift spraying on flat open country and fig. 4 shows the drop spectrum and recovery for this deposit. The deposit density is greater than 0·01 cc. per sq. m. for about 90 metres and the average dosage over this distance is about 0·03 cc. per sq. m. (about $\frac{1}{5}$ pint per acre). The most concentrated solution of dieldrin produced so far contains 0·2 g. dieldrin per cc., which would make the horizontal deposit density of dieldrin 0·006 g. per sq. m. for 90 metres. To obtain the required deposit density

(0·01 g. per sq. m.) over a large area by drift spraying with the exhaust nozzle, it would appear necessary not only to have the most concentrated oil solution possible, but also to build up the deposit by runs at calculated distances apart, which would be too complex a procedure for routine use. However, a compensatory effect comes into play when fine sprays are applied to sparse vegetation such as is typical of locust breeding areas. Drops 69 μ in diameter have a terminal velocity of about $\frac{1}{3}$ m. per sec. and in a uniform wind of 5 m. per sec. would approach the ground at an angle of 1 in 30. This means that, for such a drop size and wind speed, an isolated vertical surface should collect roughly 30 times as much spray per unit area as does a horizontal surface, since the vertical surface creates a shadow 30 times its own area (*cf.* the horizontal equivalent area (HEA) of Kennedy, Ainsworth & Toms, 1948).

Fig. 5 shows the theoretical effect of drop size and wind velocity on the pick-up

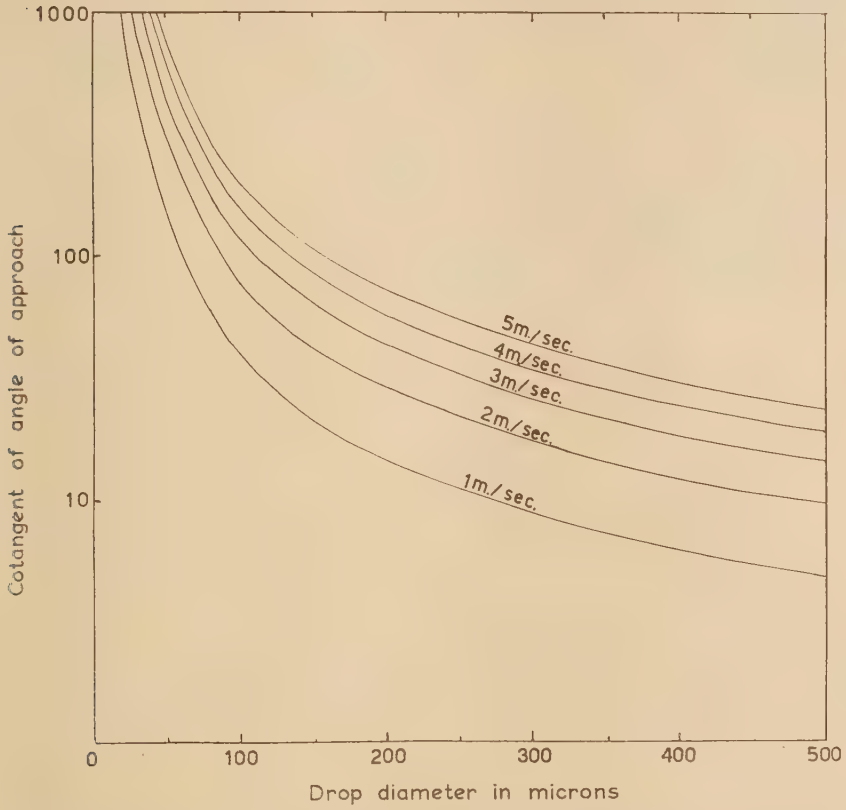


Fig. 5.—Curves showing the theoretical ratio of the deposit per unit area on isolated vertical targets to that on a horizontal surface (equal to the cotangent of the angle of approach of the spray to the horizontal) for different drop sizes at different wind speeds.

on a vertical surface relative to that on a horizontal surface, corresponding to the cotangent of the angle of approach of the spray to the horizontal ground, from which can be seen the rapid increase of this factor for drop diameters below 200 μ. The smaller drops will therefore be picked up mainly by the vegetation and a considerable increase in the deposit on the vegetation as compared with

that on the surrounding ground may be expected. Plate VII, figs. 1 and 2, show the site of spray trials against hoppers of *S. gregaria* on the Eritrean coast. In the foreground of these photographs one notices considerably more sand than vegetation, but in the middle distance the position is reversed and in the far distance only vegetation is seen. This, roughly, illustrates how the drops would be collected if emitted from the position of the camera and drift-sprayed across the area. The large drops, falling quickly, will be mainly wasted by falling on the sand, but the smaller drops will be deposited mainly on the vegetation. The actual quantity of spray that will be collected by any particular plant will depend on many factors, notably: shape and leaf area of plant, distance from next plant, distance from spray source, contour of ground, wind gradient (which is considerably affected by plant density), degree of turbulence both convective and flow, and sparseness or luxuriance of plant cover between the spray line (the line from which the spray is emitted) and the plant under consideration.

In order to estimate the relative attenuation factor (defined as the ratio of the vertical to the horizontal deposit) that could be expected in practice, the device illustrated in fig. 6 was constructed. It is essentially a sensitive wind-vane

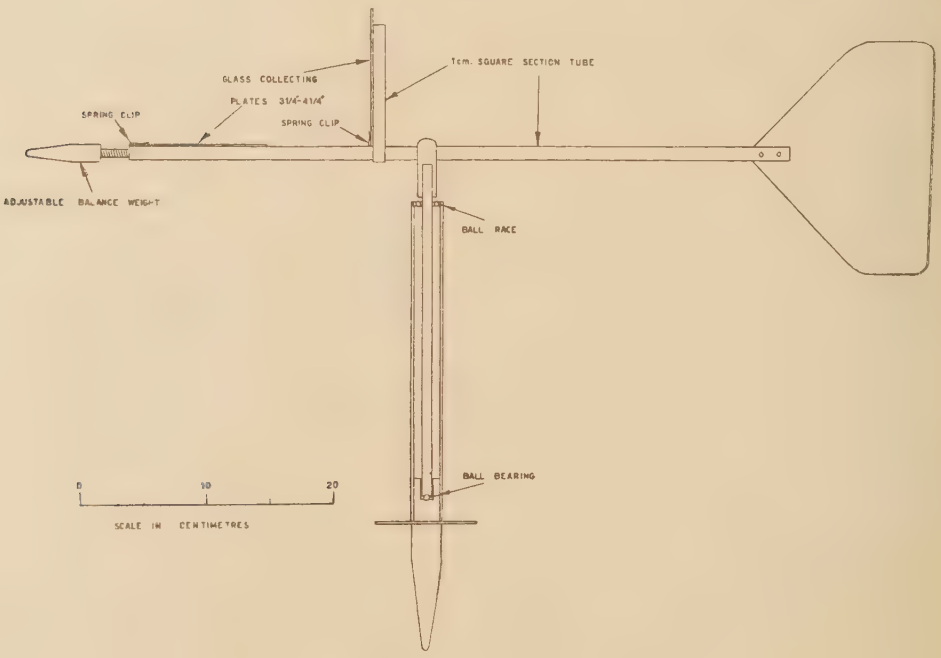


Fig. 6.—Wind-vane drop collector.

with clips to support a glass plate on the horizontal beam and another on the vertical beam. When a series of these wind-vane collectors is set up with the normal deposit-assessment layout, the ratio of the deposit on the vertical plate to that on the horizontal plate gives some indication of the increased deposit one would expect on isolated plants such as are common in desert locust areas. The results of a typical field trial using the collecting device is shown in fig. 3, and it will be seen that between 10 and 55 metres downwind from the spray line the ratio varies between about 2·5 and 8, the average being about 6·0. The

horizontal deposit density is shown together with the vertical deposit densities, and the latter are well above the theoretical minimum dosage rate for fifth-instar hoppers for over 150 metres from the spray line (not shown on the graph).

Thus, with the fine spray provided by the exhaust sprayer, the low emission rate is capable of giving on sparse vegetation a deposit sufficiently toxic and over a sufficient depth to control all instars of the desert locust. There is a lower limit to the useful drop size at about 20–30 μ, below which the drops behave more and more like a gas, flowing round vegetation and having a decreasing impaction efficiency.

Drops of the size produced by the sprayer have a large evaporative surface; the specific surface for 60-μ drops is 1,000 sq. cm., that is, 1 cc. broken down to drops of 60-μ diameter has a surface area of 1,000 sq. cm. It is not surprising, therefore, that in the early trials using dilutions with water and other fairly volatile liquids, such as kerosene, a low recovery and correspondingly low kills were obtained. To ensure recovery and also persistence of the deposit, a highly involatile diluent is clearly necessary. The oils of the Dutrex range have the desired involatility and Dutrex 3 has also good solubility for dieldrin. A 20 per cent. solution of dieldrin in Dutrex 3, although fairly stable, is, however, too viscous, and a proportion of kerosene is included in the formula to reduce the viscosity. The following formulations incorporating certain proprietary petroleum products were found to have the desired properties, but in view of the success of the field trials with the first two, no further work was carried out on the last two. Nevertheless, the latter are interesting, since the Dutrex solvents used have resinating properties and the formulations are therefore somewhat like paints, and should show very high persistence as spray deposits.

Formula A.	
Dieldrin	20%
Dutrex 3	60%
Kerosene	20%
	100%

Formula B.	
Dieldrin	20%
Iranolin KEB	72%
Iranolin 2241	8%
	100%

Formula C.	
Dieldrin	20%
Dutrex 130	20%
Iranolin KEB	60%
	100%

Formula D.	
Dieldrin	20%
Dutrex 55	30%
Iranolin KEB	50%
	100%

Formula A has subsequently been shown to be unstable on long storage at the relatively low temperatures experienced in winter at Tripoli; the kerosene has consequently been replaced by Novosol.

Field Trials against *Schistocerca gregaria.*

(a) Eritrean coast, December 1956.

A small population of hoppers on the coast of Eritrea during December 1956 gave an opportunity for limited tests of the improved spraying technique. In the first trial, on 3rd December, a single spray line was made 5–20 yd. upwind of two hopper bands (consisting of third and fourth instars), which were on the edge of and within a crop of native millet (*Pennisetum typhoides*). The spray used was Formula A and 1½ pints was emitted over 291 yd., using a prototype fine jet; this rate of emission was less than half that used in later trials when the jet was changed so as to give about 1 pint per 80 yd. By late afternoon the main band of hoppers had moved about 200 yd. roughly downwind and there was a trail of

dead all the way from the spray line. In order to obtain figures on the total number of hoppers in the bands, a further spraying, using γ BHC in oil, was carried out on 5th December over the remnants. Collection and counting of the dead hoppers showed that in the larger band, about 56 per cent. were killed by the dieldrin, of which probably only 1 pint was effective because of the path of the band. This represented a kill of about 100,000 hoppers per pint. The number killed was likely to have been limited mainly by the number of hoppers reaching the spray line.

The first trial involved both contact spraying and vegetation spraying. The second trial took place on 4th December in open country, the vegetation consisting mainly of *Dipterygium glaucum* in scattered clumps. In order to test for stomach poisoning and minimise contact effect, an area entirely downwind of a similar band of hoppers was sprayed. Three parallel spray runs about 25 yd. apart were made, again using Formula A, and 2 pints of spray were emitted over a distance of 355 yards' run, or 177 yd. per pint. The next day an area of dead hoppers extended from the last spray line more than 200 yd. downwind. Beyond this was a small live residue, the total dead being 108,000 (54,000 per pint).

The third trial took place on 15th December, in similar open country and vegetation, against two bands of fourth- and fifth-instar hoppers and fledgling adults. Three spray lines were put down during the late afternoon, using Formula B, 7·5 pints being applied over 780 yd., or about 1 pint per 100 yd. After one day, a large proportion of the largest bands was dead and by the following day a negligible proportion was left. The day after spraying, a new small band appeared and subsequently marched through the sprayed area. By the evening of the second day after spraying, this new band was entirely dead in the middle of the sprayed area. The total number of hoppers killed by the spray in this trial was 240,000, or 32,000 per pint.

These trials suggested that the number of locusts killed per pint was dependent less on the spray than on the total number of locusts present. Thus, in the third trial, there was still a large amount of sprayed vegetation that had not been traversed by hoppers, and the small number killed was due to the fact that hoppers were not present in sufficient numbers for the sprayed area to be fully exploited. The persistence of the spray shown by these trials suggested further examination of this aspect of the problem.

(*b*) *Eritrean coast, January–February 1957.*

In January 1957, egg-laying was observed on the sand-dune area known as Akbanazuf on the Eritrean coast, and a trial with the re-designed sprayer was carried out on the egg-field site before the eggs hatched, to determine the persistence of the spray formulations. It was also decided to spray, once a week, a portion of a line south and west of the infested area, where it was estimated that the marching hoppers would be when they attained the fourth and fifth instars.

Egg-field spraying.—The egg-field was situated across the Wachiro-Sheb track about three miles west of the Wadi Wachiro. The area had a new green growth of vegetation, mainly *Heliotropium pterocarpum* and *Dipterygium glaucum*, up to 18 in. high (see Pl. VII, fig. 1). A single drift-spray run was made across the site using 1 pint per 80 yd. of Formula A, at 1325 hr. on 16th January in overcast conditions and a light ENE. wind. Hoppers hatched on this site on 25th–26th January, that is, 9–10 days after spraying. Dead and affected hoppers were noticed on the 26th January, and by the 30th there were no live hoppers in the sprayed area, which extended over 200 yd. downwind of the spray line, there being very many dead. There is little doubt that all the hoppers that had hatched in the sprayed area, or passed through it, had died.

Hopper bands.—Hatching over most of the area under observation took place about the 24th–25th January. On 30th January, a survey was made of a large number of bands to the south-west of the sprayed egg-site in order to determine where to put the spray lines so that the hoppers would cross them in a later instar, preferably the fourth or fifth. The extent of these bands, which included also many scattered hoppers, was marked both with coloured and numbered flags and with marks on the ground made with a mixture of white gypsum and various coloured pigments. It was hoped to follow and mark each day the movement of these bands so that the direction and rate of marching could be determined. However, it was also desirable to carry out some spraying immediately, in order to obtain as long a period as possible between spraying and the crossing of the spray lines by marching bands. It was decided, therefore, to put down some spray across the general direction in which bands were already moving. On 31st January, three spray runs were made in positions about 5,000 yd. south and south-west downwind of the egg-field area. In these three spray runs, the same insecticide and machine settings were used as had been used at the egg-site, the emission rate being 8 ml. per m., and Plate VII, fig. 2, shows a part of the sprayed area. The vegetation here was thinner and shorter than that at the egg-field site, being 6–12 in. high. The whole area was watched on the following days, and by 5th February it had become obvious that the area of infestation and the number of bands in it were greater than had previously been thought, and also that the rate of movement was much faster. On 6th February, bands started crossing the spray lines and moving between them. A large band, 300–400 yd. in extent, crossed the centre spray line on this day (six days after spraying) on a south-south-west course. By 9th February, this band had almost completely died; the few stragglers were destroyed by birds. On the 7th, another, smaller band crossed this line and it too subsequently died.

On 10th February, a very large band crossed the spray line and a considerable part of it, though not all, had died by the evening. By now most of the bands in the area were being attacked by an ever increasing number of birds, mainly kites, and it was becoming impossible to assess the effect of spraying since any affected and straggling hoppers were being eaten; also, bands were being reduced by the birds to non-marching, isolated groups of hoppers. Consequently further experiments were abandoned.

The limited results obtained showed that the spray used could, at least in some cases, persist for over 6–7 days, sufficiently long to cause a very high mortality amongst second- or third-instar hoppers after this period. The incomplete kill obtained on a large band that crossed the west spray line on 10th February is probably explained by the fact that the strength of the wind during the spraying here was unsuitable. It was thought that with a cross wind of 8–10 m.p.h., there would have been sufficient depth of sprayed area to cope with the large bands. The proportion of this band that died from eating sprayed vegetation (estimated at two-thirds) probably represents the number that could find enough vegetation to eat in the sprayed area. Most of the bands ate all the leaves of the vegetation through which they marched, and could easily be tracked by this fact. Calculations from laboratory figures for LD90 and from the measured spray deposits suggest that the hoppers that died must have been heavily over-dosed.

(*c*) *Tripolitania, May–June 1957*.

The results of the previous trials, against small-scale infestations, made it highly desirable to try the machine and technique on a major infestation. An opportunity to do so occurred when the Libyan Government offered facilities and reserved an area for trials on the coastal plains of Libya during May and June 1957. The area chosen was typical dune country around El Hebilia Fort (32°25′N., 11°50′E.) about 150 km. west-south-west of Tripoli and 70 km. from the coast.

The vegetation of this typical Gefara desert-steppe country included *Artemisia campestris*, *Retama raetam*, *Rhanterium malveolens*, *Salsola* sp., *Asphodelus pendulinus* and *Delphinium* sp. Hatching had been reported in this area on 2nd May.

Limited quantities of Formula A were available and these were used on three small-scale trials in the vicinity of the camp site, which was 3·7 miles east-north-east of Hebilia Fort.

In Trial 1 and Trial 3, spray lines were again applied clear of the band on the downwind side, to test stomach action. In Trial 1, three parallel spray runs were made across wind and about 50 yd. apart. A total of 5½ pints of Formula A was used over 0·4 miles, making an emission rate of 1 pint per 127 yd. This lower emission rate was due to filter blockage by rust, a trouble that was eliminated in subsequent trials. The band changed its direction of march after the spraying and crossed only about 50 yd. of the first spray line. Trial 3, a day later, was again aimed at spraying ahead of this band, two spray lines 50 yd. apart being put across the line of march, and on this occasion the emission rate was 1 pint per 77 yd. Again, full interception of the band was not achieved, but dead were seen the next day under the sprayed vegetation that had been crossed by the band. In Trial 2, a band was sprayed in the morning while still basking and some contact action was to be expected. These spray runs were made, across the wind and 50 yd. apart, over the area occupied by the basking hoppers, the emission rate being 1 pint per 77 yd. The band left the site soon after the spraying, and dead were found scattered along its path up to more than 400 yd. from the sprayed area. The remnants crossed the path of a much larger band, so that it was not possible to assess fully the results on the original target.

No other control measures were carried out in the vicinity of these three spray sites, which were examined regularly during the following 3–4 weeks. During most of this period, further scattered hoppers, and later fledglings continued to invade the area, and at almost every inspection freshly dead and affected hoppers were seen. The sites were finally inspected 26 days after the spraying, and under the sprayed clumps of vegetation many affected and dead fledglings were seen. Two nights of very heavy rain were experienced, and also periods of ' Ghiblis ', which are characterised by hot sand-bearing winds with velocities up to 20 m.p.h. and temperatures of up to 110°F.

Larger-scale operations were undertaken to test the effectiveness of the method under the conditions of an actual campaign. Between 25th May and 10th June a total of 1,570 litres of an improvised 10 per cent. dieldrin formulation (1 Imp. gal. Dieldrex 15 to 1 U.S. gal. S.A.E. 20 motor oil) was applied to large bands, most of them more than one sq. km. in extent, of fourth- and fifth-instar hoppers and fledglings. Detailed assessments of representative operations provided objective evidence confirming visual impressions of the highly satisfactory kills obtained. Thus, two days after the spraying operations of 2nd June around Km.36 on the Zuara-El Uotia road, counts at a large number of regularly spaced points representing the whole area sprayed on that occasion gave an average of 19 dead fifth-instar hoppers per sq. m. over an area of 0·7 sq. km. as a result of the application of 144 litres of 10 per cent. dieldrin. This gives a kill of about 93,000 hoppers per litre of 10 per cent. spray. Another assessment was made similarly near Ben Gaied, and this gave a kill of about 47,000 fourth-instar hoppers per litre on the sprayed site.

(*d*) *Ogaden, Ethiopia, November 1957.*

All the previous trials had been carried out in open semi-desert country such as is typical of a large part of the desert locust terrain, but not of the particular terrain that is the main breeding area producing the swarms of locusts that invade East Africa. These swarms arise from breeding in the Somali Peninsula

and the hopper bands in this case infest very extensive areas of arid thorn-bush country (see Pl. VIII).

In November 1957, a large-scale infestation had developed in such bush country around Wardere in the Ogaden region of Ethiopia. A hundred gal. of Formula A and the same amount of Formula B were used with exhaust-nozzle sprayers during the control campaign, as also was 150 gal. of a formulation of Dieldrex and oil (S.A.E. 20). Numerous spraying operations were undertaken against individual hopper bands, the technique being to make two or three cross-wind runs ahead of and in the line of march of the bands. This technique was consistently successful in killing the target band, and it killed other bands arriving on the same site later. An egg-field site was sprayed fourteen days before hatching, again with complete control in the sprayed area. During the target-spraying operations, it was observed that the Wardere-Eldere and the Wardere-Scillave roads were being crossed regularly by hopper bands. Accordingly, a single spray line was made along about 32 km. of each road and both Formula A and Formula B were used. The spray runs were made as and when opportunity occurred and were completed over a period of several days; various weather conditions were thus encountered during the spraying operations. The sprayer emitted 8 to 10 litres per km. (3 to 4 gal. per mile) proceeding at 8 km. per hour (5 m.p.h.). The sprayed roads were examined almost daily over the ensuing weeks of the hopper infestation, and records made of the hopper bands that were seen to be crossing them and becoming affected by the spray. On several occasions, bands of hoppers were followed after they had crossed the road, and on no occasion when this was done were any survivors observed. Eventually, both sprayed roads became lined continuously with dead second-, third- and fourth-instar hoppers, (see Pl. VIII) except for about 5 km. on the Eldere road. In general, the dead were dense over about 200 m. of ground to one side of the road and 20–50 m. on the other. In one place, dense dead were observed over 600 m. to the south of the Eldere road. In several places successive layers of dead were seen, newly dead fourth-instar hoppers being superimposed on dried dead hoppers in the third and second instars. Forty days after spraying, dead and dying fledglings were observed on the Scillave road.

Towards the end of the control campaign, when a nearby area was overrun by fifth-instar hoppers, an attempt was made to see what output could be achieved by a single sprayer operated by one man. During two days, some 475 litres of spray were applied during 10 hours along 40 miles of a network of tracks near Eldere where there was an almost continuous fifth-instar infestation of the area, sometimes dense bands and sometimes thinly scattered individuals.

Conclusions.

The results of the field trials demonstrate that by drift spraying with very fine drops of involatile insecticide solutions, it is possible to produce toxic deposits on sparse vegetation typical of both desert and bush in which the desert locust breeds. Two techniques may be used; both involve the spraying of vegetation which it is judged will subsequently be eaten by hoppers, but 'target' spraying is done on or near a hopper band, whereas 'barrier' spraying is done, not necessarily in sight of hoppers, across an area known to be highly infested. The exhaust-nozzle sprayer has been proved effective and reliable for producing suitably toxic spray deposits, from single spray lines with an emission rate of as low as 8 cc. per metre run. The special formulations developed for the spray technique have been shown to have a persistence of at least 40 days over a wide range of climatic conditions, ranging from hot desert winds to tropical rainstorms, and this persistence can be exploited by the making of spray barriers. Such spray barriers, made along roads by ground-spraying machines, could usefully add to

any control campaign in an area of high infestation. In certain areas such as open desert steppe, where the terrain presents few obstacles to motor vehicles, it would be possible to build up a series of parallel cross-wind spray lines which would need to be made only close enough to ensure that nearly all the hoppers in the area would cross at least one line during their marching life. The distance apart would be related to the distance likely to be covered by a band between hatching and reaching the fledgling stage, which was about 15 miles in the case of the large bands studied in Libya. For the Ogaden, such information has so far been recorded for only two bands, one small (covering about 0·1 acre) which travelled 2 miles during its life, and one large (covering about 3 acres) which travelled 12 miles (Ellis & Ashall, 1957). Full exploitation of this new technique demands much more information on this point and especially on whether there is any tendency for the hopper displacement to be biased down the most prevalent wind, as was the case during the trials on the Eritrean coast. Such a tendency would permit a very open pattern of spray lines, with a corresponding economy of effort and an extension of areas covered.

In considering the possibilities of further development of this spraying technique, it is necessary to appreciate that, in major breeding areas like the Ogaden and the adjoining territories, heavy hopper infestations can, as in 1957, extend over an area of the order of 100,000 sq. km. of this bush country. Even where tracks are available, each exhaust-nozzle sprayer is unlikely to achieve an average rate of application of more than about 30 km. of spray line per day; and, for producing the regularly-spaced pattern of spray lines needed to exploit the full possibilities of barrier spraying, the effectiveness of any ground machine in such terrain must be severely limited both by difficulties of accurate cross-country navigation and by the actual impassability of some areas of bush. It is considered that the best prospects of effective control under such conditions of terrain and of scale of infestation are offered by the extension of the barrier-spraying technique by the use of aircraft, provided that spray gear and tactics can be developed to produce, from the air, a spray line comparable in performance with that given by the present exhaust-nozzle sprayer.

Toxic Hazards.

Highly concentrated solutions of dieldrin in oil, such as have been used in the trials here described, present potential toxic hazards to personnel handling them in the field and to stock grazing on the sprayed areas. Contamination of personnel must be minimised by suitable handling and spraying procedures, and any accidental contamination must be immediately removed. Trials to investigate potential hazards to stock were carried out by Ashall and Hemming on typical locust-breeding areas in the Northern Frontier Province of Kenya. In each trial, eight sheep and eight goats were tethered by a 10-yard rope in the sprayed area at 10, 30, 50 and 70 yd. from the spray line: in the first experiment, two spray runs along the same line were made with the animals already in position, but in the second, six repeated spray runs were made before tethering the animals in the sprayed area. One animal died seven days after test, from lung haemorrhage, believed attributable to pneumonia, and not considered as due to dieldrin. A second animal, seven days after spraying, exhibited a minor convulsion, which may have been attributable to dieldrin, but subsequently recovered. With these dosages of two and six times the normal, and with the animals restrained to the area for seven and five days, respectively, there appear to have been no deaths attributable to the dieldrin. These tests, together with evidence of maximum tolerable basic dosages, indicate that there is an ample margin of safety when using dieldrin applied by this spray technique for the control of locust hoppers.

Summary.

Studies of the physical and biological factors involved in the application of concentrated involatile oil solutions of a persistent insecticide (dieldrin) in the form of a fine spray to the low-density vegetation typical of the breeding areas of the desert locust, *Schistocerca gregaria* (Forsk.), have led to a technique of control of the locust hoppers with a dosage as low as 0·30 litres per hectare (approximately $\frac{1}{5}$ pint per acre). A simple device for producing such a spray has been designed to work off the exhaust system of a light four-wheel-drive motor vehicle. Successful control of hoppers has been obtained under a wide variety of weather conditions in both desert and bush typical of locust breeding areas, using ' target ' and ' barrier ' spraying techniques. Both techniques involve the spraying of vegetation which it is judged will be subsequently eaten by the hoppers, but target spraying is done on or near a known hopper band, whereas barrier spraying is done, not necessarily in sight of hoppers, across an area known to be highly infested. Examples of such successful attacks are described from the Eritrean coast, Tripolitania and Ethiopia. The methods can replace the well established technique of poison-baiting individual bands, and have the additional advantage of producing highly persistent toxic swathes which can be exploited by the barrier technique for treating locust egg-fields and for creating widely spaced barriers for the control of extensive infestations.

Acknowledgements.

The author is greatly indebted to Mr. P. R. Stephenson, Director of Desert Locust Survey, Nairobi and to Dr. B. P. Uvarov, F.R.S. and Dr. T. H. C. Taylor, respectively past and present Directors of the Anti-Locust Research Centre, London, for their encouragement and support of this work. In the field, much of this work would not have been possible but for the active assistance of many people, and the author is particularly grateful to the following: Dr. R. C. Rainey, Messrs. C. Ashall, H. R. McMichael, T. Spence, P. Hay, P. R. Stewartson, T. Reeves and Sig. U. Amarante, all of the Desert Locust Survey, East Africa High Commission; the Nazir, the Director of Agriculture (Mr. E. Sicely), and Messrs. Omran Azzabi and Giuma Giaddaui of the Department of Agriculture, Tripolitania; Mr. H. A. Lillingston of Shell International Chemicals Ltd.; and Mr. R. J. Courshee of the National Institute of Agricultural Engineering.

References.

Courshee, R. J. (1955). Further trials of drift spraying for locust control.—*Dep. Note nat. Inst. agric. Engng* no. 54.

Courshee, R. J. (1959). Drift spraying for vegetation baiting.—*Bull. ent. Res.* **50** pp. 355–370.

Ellis, P. E. & Ashall, C. (1957). Field studies on diurnal behaviour, movement and aggregation in the desert locust (*Schistocerca gregaria* Forskål).—*Anti-Locust Bull.* no. 25, 94 pp.

Kennedy, J. S., Ainsworth, M. & Toms, B. A. (1948). Laboratory studies on the spraying of locusts at rest and in flight.—*Anti-Locust Bull.* no. 2, 64 pp.

Lhéritier, G. (1955). Essais de moyens de lutte contre la sauterelle pèlerine (*Schistocerca gregaria* Forsk.).—*Trav. Serv. Déf. Vég. Maroc* no. 8, 20 [+28] pp.

Osborne, F. W. (1956). An exhaust sprayer for locust control.—*J. Dep. Agric. S. Aust.* **59** pp. 268–270.

Pearson, A. J. A. [1958]. The toxicity of dieldrin to the later instars of the desert locust, *Schistocerca gregaria* Forsk.—*Shell agric. Bull.*, no. ADB: 620/Fb.18, 14 pp.

Sayer, H. J. & Rainey, R. C. (1958). An exhaust-nozzle sprayer for ultra-low-volume application of persistent insecticide in locust control.—[4] pp. London, Anti-Locust Res. Cent.; E. Afr. High Comm., Desert Locust Surv.

Toms, A. M. & Goodman, A. (1957). The importance of drift in insecticide spraying experiments: some observations from insect behaviour in cotton.—*Emp. Cott. Gr. Rev.* **34** pp. 177–188.

© Commonwealth Agricultural Bureaux, 1959.

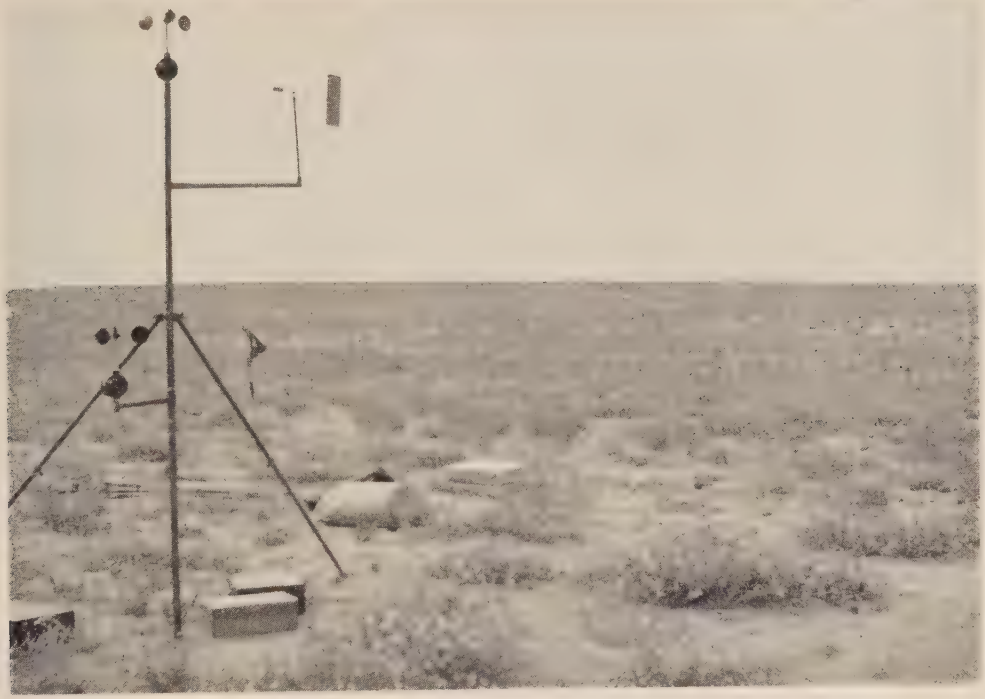


FIG. 1. Site of the egg-field spraying trial on the Eritrean coast.

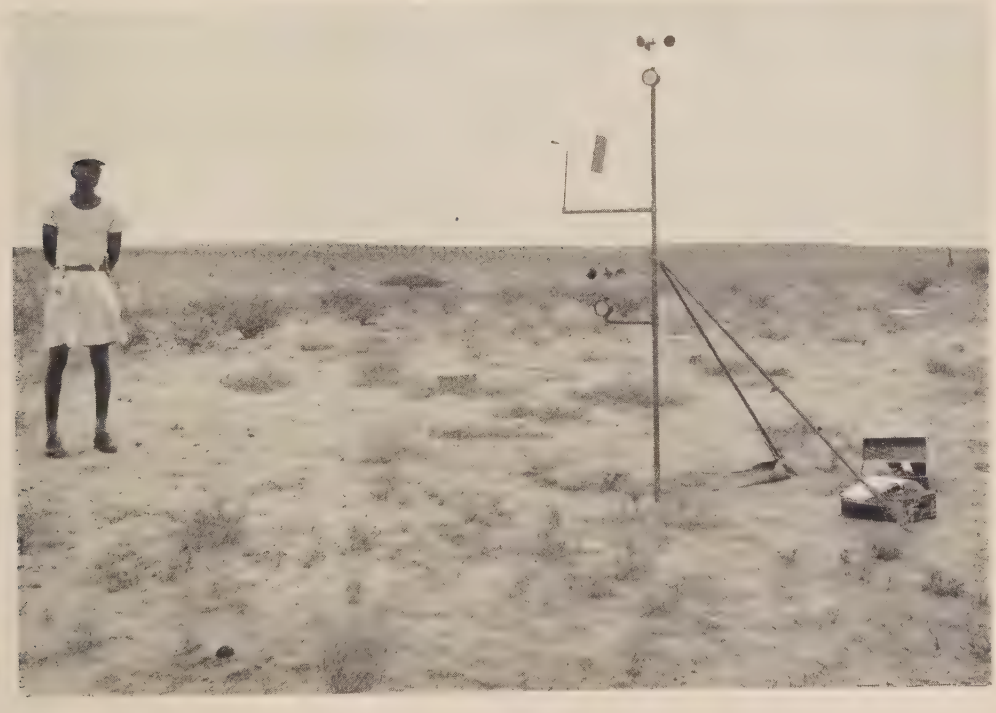


FIG. 2. Part of the area on the Eritrean coast in which the trials of spray-lines against hopper bands were conducted.



Dead third-instar hoppers on the spray barrier on the Wardere-Eldere road. Hoppers were lying dead at this density up to 200 yd. from the road. The bush is typical of this part of the Ogaden.

AN ANALYSIS OF THE EFFECTS OF TEMPERATURE UPON THE GROWTH AND REPRODUCTION OF *DYSDERCUS FASCIATUS* SIGN. (HEMIPTERA, PYRRHOCORIDAE).

I.—THE INTRINSIC RATE OF INCREASE.

By Kenneth U. Clarke and Jaivant B. Sardesai *

Department of Zoology, University of Nottingham.

(Plate IX.)

In a preliminary investigation of the effects of temperature on the growth and reproduction of *Dysdercus fasciatus* Sign., the birth rate and mortality rate were calculated, thus giving values of the intrinsic rate of increase. Consideration of the data suggested that it would be profitable to use this parameter as a single statement about the effects of temperature on growth and reproduction, and to regard the factors actually measured as components in the analysis of this concept. By doing this, a more satisfactory integration is effected of measurements on birth rate, mortality rate, fecundity, fertility and growth than is generally the case in laboratory studies of insect cultures.

There is a major difficulty in applying the concept of the intrinsic rate of increase to cultures of *D. fasciatus* reared under constant environmental temperatures. It is a difficulty likely to be encountered in any insect all of whose stages do not survive under the same environmental conditions. Under the conditions of the experiments, the eggs of *D. fasciatus* hatched at only three of the temperatures tested, namely, 25, 28 and 30°C. Post-embryonic development, however, was completed under a wider range of temperature, namely 20–30°C. The relative humidity was maintained at 60 per cent. at all temperatures except 28°C., at which it was 70 per cent. To allow comparison of data on growth and reproduction at temperatures lying outside the embryonic range, this stage was ignored and mortality rate and generation interval were measured from the time of hatching, the embryos being reared under optimum conditions and moved to the appropriate temperature within an hour of hatching.

This procedure gives a restricted meaning to the concept of the intrinsic rate of increase, but is thought to be justified as a device by which a wider range of conditions could be compared.

Material and Methods.

Stocks of *D. fasciatus* were kept in an insectary at 28 ± 1°C. and 70 ± 5 per cent. relative humidity. The photoperiod was 12 hours' light alternating with 12 hours' darkness. A large number of observations was made on insects reared under these conditions, which will be referred to hereafter in this paper by their temperature characteristic, 28°C. For temperatures of 15, 20, 25, 30, 35 and 40°C., smaller cages were used. Each cage had its temperature kept constant to within ± 0·25°C., a relative humidity of 60 ± 3 per cent., a photoperiod similar to that mentioned above, and a light intensity of 50 foot-candles at the

* The data given in this paper were obtained by the junior author as part of the requirement for the degree of M.Sc. at the University of Nottingham.

centre of the cage. Air was circulated in each cage by a fan, the air speed being 50–82 metres per minute in the centre of the cage.

The insects were kept in perforated-zinc boxes suspended in the middle of each cage. Except where otherwise stated, abundant food, in the form of cotton seed, was always available to the insects. Water was supplied in plastic tubes perforated with a small hole plugged with a wick, which projected slightly from the surface. The insects took water freely from the wick, and the amount that evaporated did not influence the relative humidity.

Calculation of Intrinsic Rate of Increase.

The primary data needed for the calculation of the intrinsic rate of increase were an age schedule of births and of deaths. The former was constructed by observing daily the number of eggs laid by a female kept with a male throughout the whole of her adult life, and results are given as the number of eggs laid per female per three days. The latter was constructed by observing daily the number of deaths occurring in a sample, from the moment of hatching until the death of the last individual; the results are given as the probability at birth of being alive at the end of each instar and each three-day interval during adult life. Graphical representation of this data for temperatures 20, 25, 28 and 30°C. is given in fig. 1. One sample, consisting of 20 individuals, was used for each temperature.

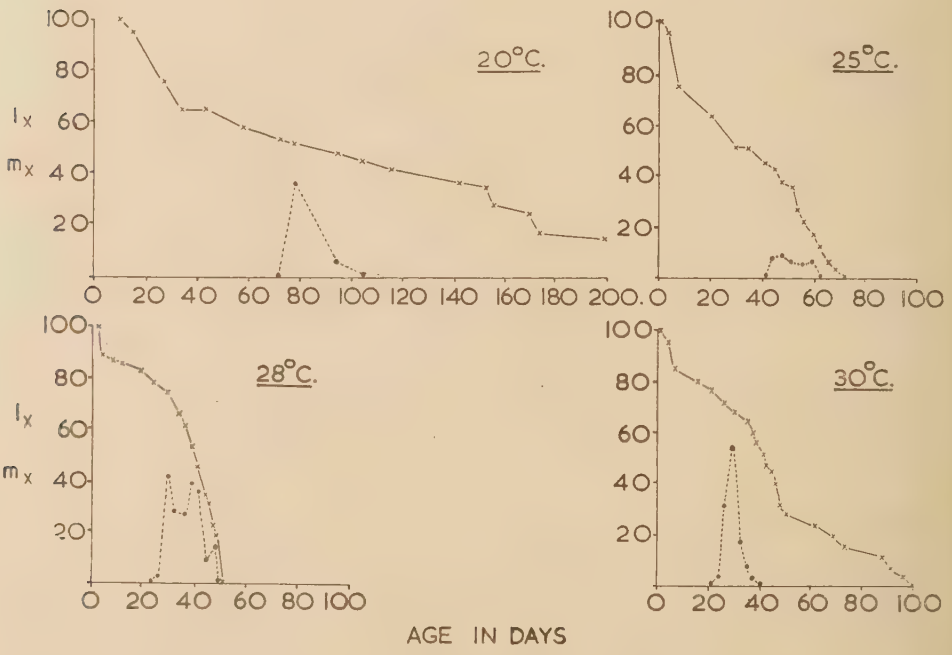


Fig. 1.—The survival rate and rate of egg-laying for populations of *Dysdercus fasciatus* reared at different constant temperatures. x——x, l_x (probability of being alive at time x); ●- - -●, m_x (eggs per female per three days at time x).

The intrinsic rate of increase (r) was calculated from this data using the formulae, symbols and definitions given by Birch (1948). The method used is given below.

The interval in days between generations (T) was calculated from the formula

$$T = \frac{\Sigma\, x\, l_x\, m_x}{\Sigma\, l_x m_x} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ (1)$$

where x represents the time in days since hatching, l_x the probability of being alive at time x, and m_x the number of eggs laid at time x.

With the value for T given by (1), an approximate value for r was calculated as

$$r = \frac{\log_e R_o}{T} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ (2)$$

where R_o, the net reproduction rate, is the summation of the product $l_x\ m_x$. Using r from equation (2) as a guide, r was then solved, by the method of successive approximations, in the equation

$$\int e^{-rx} l_x m_x = 1 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ (3)$$

The interval between generations was then recalculated using the more precise value for r from equation (3), thus

$$T = \frac{\log_e R_o}{r} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ (4)$$

This is the value for T given in Table I.

TABLE I.

Calculated values of r, λ and T for populations reared under given constant temperatures.

	Temperature (°C.)			
	20	25	28	30
r ..	0·259	0·322	0·812	0·924
λ ..	1·29	1·38	2·25	2·52
T ..	80·48	56·84	41·79	34·02

r, intrinsic rate of increase per week; λ, finite rate of increase per week; T, generation interval in days.

The stable age-distribution for the values of r at different temperatures, together with the contribution that each age-group of the reproductive phase makes to the value for r, was also calculated, following closely the methods given by Birch (1948).

The values for the intrinsic rate of increase, the finite rate of increase (λ) and the generation interval are given in Table I. The stable age-distribution for these values of r is given in Table II and the contribution each age-group makes to r in Table III.

The effects of temperature upon these factors can be summarised as follows:—

(a) The value of the intrinsic rate of increase increases with increasing temperature; the highest value obtained is that for the highest temperature at which development was completed.

(b) The interval between generations decreases as the temperature increases. This is a simple straight-line relationship, such that for every 1°C. rise in temperature within the range 20–30°C. the generation length is shortened by 4·6 days.

(c) At 20°C., the first age-group of the adult stadium contributes most to the value of r. As the temperature increases, later age-groups become relatively more important and at 30°C. it is the third age-group that makes the greatest single contribution to r.

TABLE II.

The stable age-distribution for values of r given in Table I. Results are given as a percentage distribution, and values in the adult stadium represent successive three-day intervals (numbered 1 to 13).

Age-group	Temperature (°C.)			
	20	25	28	30
1st instar ..	15·14	17·27	17·63	18·93
2nd instar ..	13·09	15·35	14·06	15·76
3rd instar ..	9·97	11·81	12·11	12·34
4th instar ..	8·32	9·47	10·61	10·18
5th instar ..	8·02	7·32	9·22	8·40
Adult 1 ..	6·54	6·99	7·67	7·12
2 ..	6·17	5·89	6·68	5·98
3 ..	5·63	5·25	5·79	5·01
4 ..	5·11	4·78	4·80	4·19
5 ..	4·61	4·45	3·66	3·44
6 ..	4·05	4·03	3·00	2·76
7 ..	3·62	3·53	2·29	2·11
8 ..	3·21	1·59	1·53	1·23
9 ..	2·47	1·23	0·89	0·94
10 ..	2·13	0·63	—	0·71
11 ..	1·47	0·34	—	0·41
12 ..	1·18	—	—	0·27
13 ..	—	—	—	0·07
	100·72	99·93	99·94	99·65

(d) When plotted upon a semi-log plot (Deevey, 1947), the survival curve shows an almost ideal distribution at 28°C. (fig. 2). At 20°C., the survival curve tends to be straightened, indicating that at this temperature death is almost independent of age. This rather unusual situation

TABLE III.

The contribution made by each age-group of the adult stadium to the value of r. Results are given as a percentage distribution, and the age-groups represent successive three-day intervals.

Adult age-group	Temperature (°C.)			
	20	25	28	30
1 ..	91·6	32·1	3·4	8·4
2 ..	8·4	29·8	48·3	38·7
3 ..	—	16·8	21·2	42·0
4 ..	—	11·4	11·6	7·3
5 ..	—	9·7	10·8	2·5
6 ..	—	—	6·2	0·8
7 ..	—	—	0·7	0·9
8 ..	—	—	0·7	—
	100·0	99·8	102·9	100·6

has been confirmed in later work, and the causes of death at this and lower temperatures are being further investigated in this laboratory.

(e) The age-schedule of births (eggs per female per 3 days, see fig. 1) shows that at 28°C. a high rate of egg-production lasts longer than at other temperatures.

It is convenient to deal with the further analysis of the intrinsic rate of increase under two headings: post-embryonic growth, and reproduction.

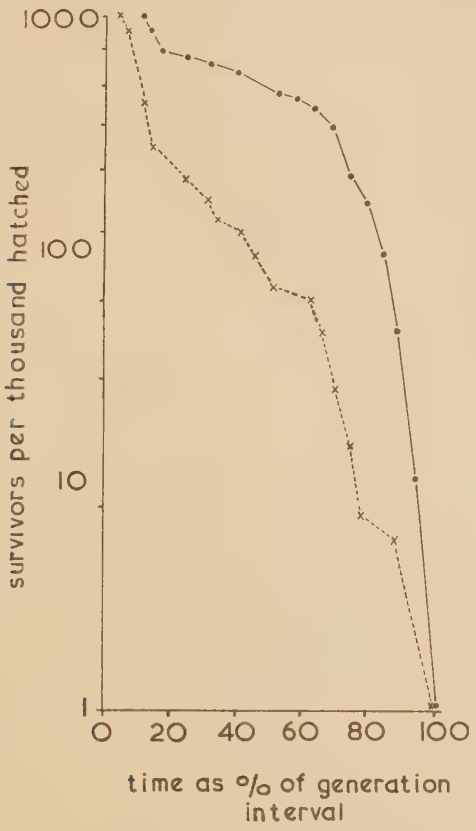


Fig. 2.—Semi-log plot of the survival (expressed as the number of survivors per 1,000 individuals hatched) against time (expressed as a percentage of the generation interval) for populations of *Dysdercus fasciatus* reared at different temperatures. x - - - x, survival curve for 20°C.; ●——●, survival curve for 28°C.

Post-embryonic Growth and Survival.

Studies of growth were carried out over many generations of the insect. Since data given by Pomeroy & Golding (1923) had suggested that in *D. superstitiosus* (F.) there was a distinct lengthening of the life-cycle after the second filial generation, it was thought worth while to see if such a difference occurred also in *D. fasciatus*.

For this purpose, ten successive generations were reared at 28°C. and ten samples, each of 50 individuals, were measured from each generation; their

percentage survival up to the commencement of adult life, weight at this time, duration of post-embryonic development, and sex-ratios were recorded. Results for the first three generations and the tenth are given in Table IV. Statistical analysis was carried out to compare the lengths of post-embryonic development for generations F_1 and F_2, F_2 and F_3, F_1 and F_3 and F_1 and F_{10}, using the formula given by Chambers (1945). No difference at the 5 per cent. level of probability

TABLE IV.

The characteristics of growth for four out of 10 successive generations of *D. fasciatus* reared at 28°C. and 70 per cent. relative humidity.

Generation	Duration of each instar in days						Survival (%) to adult stage	Sex ratio	Weight (mg.)	
	Instar									
	Egg	I	II	III	IV	V		♂♂ ♀♀	♂♂	♀♀
F_1 ..	6·2	3·1	4·3	4·5	4·7	7·8	77·6	1 : 1·1	55·0	98·0
F_2 ..	5·9	2·9	4·1	4·3	5·2	7·1	77·1	1 : 1·2	52·0	103·0
F_3 ..	6·2	2·9	4·3	3·8	5·0	7·5	76·0	1·5 : 1	56·0	101·0
F_{10} ..	6·1	3·0	4·0	4·2	5·0	8·0	76·0	1 : 1·2	60·0	103·0
Mean ..	6·1	2·97	4·17	4·2	4·97	7·6	76·67		55·75	101·2

was found. Comparison of the weights of the newly moulted adults similarly showed no significant differences. It is therefore concluded that Pomeroy & Golding's conclusions for *D. superstitiosus* do not apply to *D. fasciatus*.

Examination of the data obtained on the growth of *D. fasciatus* suggested that the following factors were important because of their influence on the intrinsic rate of increase: the growth rate, the size of the animal just after the last ecdysis, and the causes of death.

The effect of different constant temperatures upon the duration of each instar of *D. fasciatus* is given in Table V. For temperatures at which the embryo failed

TABLE V.

The effect of temperature upon the duration of each instar of *D. fasciatus* (mean values in days of 20 individuals of each instar at each temperature).

Instar	Temperature (°C.)					
	15	20	25	28	30	35
Egg ..	—	—	6·4	6·1	5·4	—
1st instar	13·0	6·0	4·0	3·0	3·0	3·0
2nd instar	16·0	10·7	8·0	4·2	4·6	4·6
3rd instar	—	7·4	6·1	4·3	4·2	5·0
4th instar	—	9·1	6·8	4·8	5·9	9·0
5th instar	—	16·3	10·3	7·5	7·4	—
Total ..	—	—	41·6	29·9	30·5	—

At 40° C., none of the insects lived longer than one day.

to complete its development, the figures refer to insects whose embryonic life was passed at 28°C.

Embryonic development was not completed at 15, 20 or 35°C., nor was post-embryonic development at 15 or 35°C. All the insects died during the early part of the third instar at 15°C., and during the early part of the fifth instar at 35°C. At 40°C., all stages died within 24 hours.

Growth during the first instar at different temperatures in shown in fig. 3.

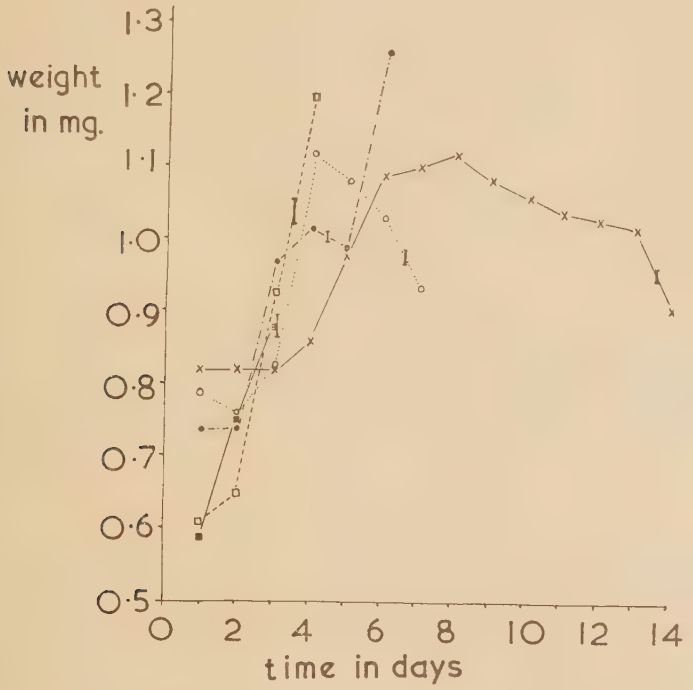


Fig. 3.—The increase of weight during the first stadium and immediately after the first ecdysis of nymphs of *Dysdercus fasciatus* reared at different temperatures. Each point represents the mean weight of a sample of 25 individuals. The vertical line across each curve represents the time of ecdysis. x——x, 15°C.; o . . . . o, 20°C.; ●— · — · —●, 25°C.; □ - - - □, 30°C.; ■ —— ■, 35°C.

Each point represents the mean of 25 individuals weighed simultaneously. Growth of individual insects from the commencement of the second instar to the end of the fifth instar is shown in fig. 4. Each graph represents the growth of one of 20 individuals studied for each temperature. Separate records were kept for each individual, and the one figured is that judged typical for its group, by comparison with others of its kind.

From fig. 3 it can be seen that during the first instar the rate of growth (measured in terms of live weight) increases with the temperature, while the interval between the peak weight and the first ecdysis becomes shorter and, at 30°C., disappears. In fig. 4, a similar change is shown for growth from the second instar to the last ecdysis at temperatures of 20, 25 and 30°C. At 15°C., little growth occurs during the second instar, although the insect lived for 17 days. At 35°C., growth is rapid at first and slows down later; very little growth occurs

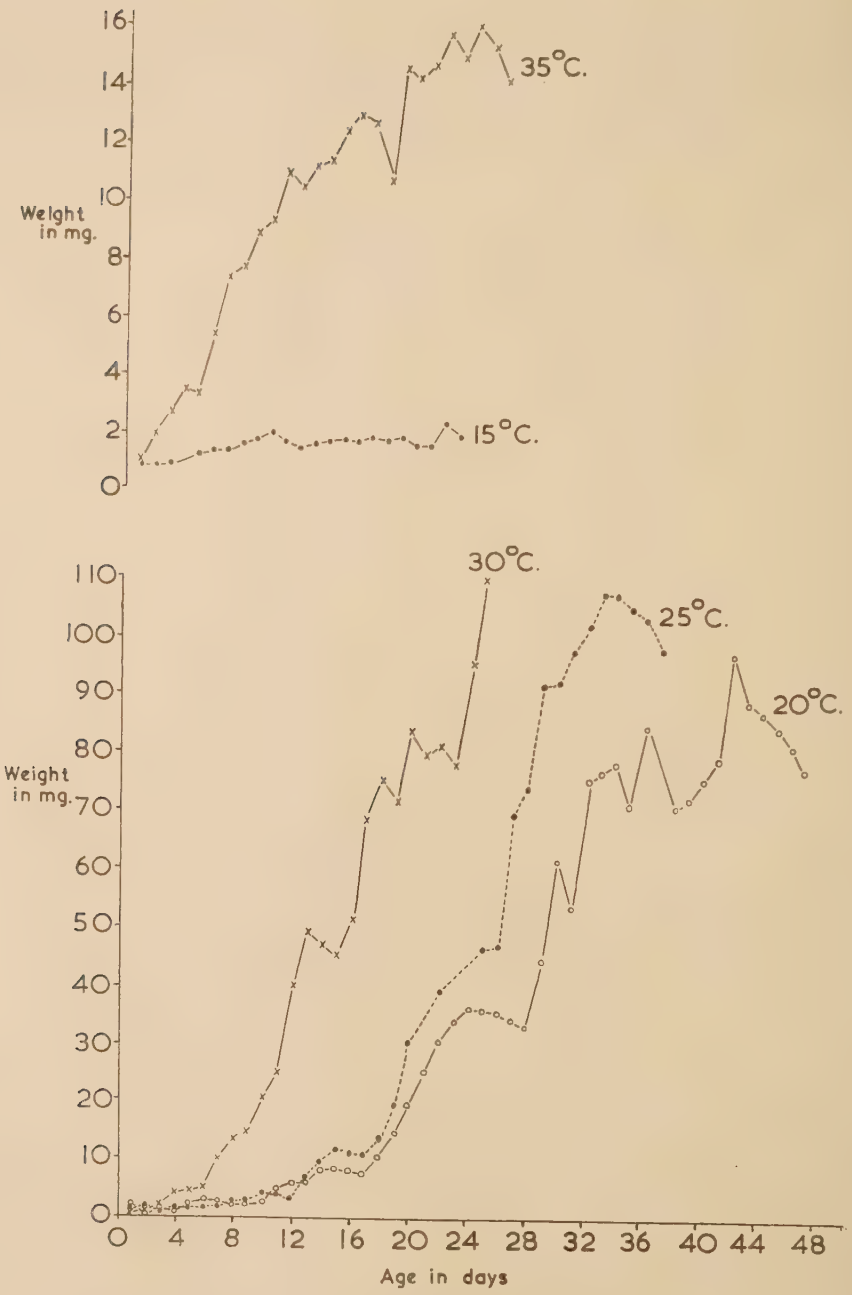


Fig. 4.—Growth curves for individual examples of *Dysdercus fasciatus* reared at different constant temperatures. Each curve represents the live weight of one individual, determined daily from the beginning of the second instar to the adult stage, the last point in each curve being that for the newly moulted imago.

during the last part of the fifth instar and the final weight is much less than that reached at lower temperatures, being about one-fifth of that reached at 20°C. and one-eighth of that reached at 30°C.

The final size reached by insects reared at different temperatures, as represented by the live weight of the recently moulted adult, is given in Table VI.

TABLE VI.

The final size of insects reared at different constant temperatures, as indicated by the weight immediately following the last ecdysis.

Temperature (°C.)	No. of individuals in sample	Mean weight (mg.)	
		♂	♀
20	20	60·3 ± 8·3	84·9 ± 10·7
25	20	58·9 ± 7·4	114·8 ± 12·6
28	40	55·7 ± 8·6	101·2 ± 13·0
30	20	52·6 ± 9·1	94·4 ± 8·9

Compared with differences caused by other factors, those due to temperature appear to be of little significance; as shown in Table VII, the size of the adult is considerably affected by the amount of water made available to it during its period of growth. The importance of the absolute size reached by the adult will be apparent from the section upon reproduction (see p. 398).

TABLE VII.

The final size of insects reared at 28°C. and 70% R.H., with restricted supplies of drinking water, as indicated by the weight (in mg.) immediately following the last ecdysis.

Sex	No. of individuals in sample	No. of hours per day for which water available		
		24	6	1
♂ ..	10	54·6 ± 8·8	40·86 ± 6·1	32·1 ± 7·3
♀ ..	10	100·2 ± 9·0	68·6 ± 7·8	44·5 ± 6·8

The factors responsible for some 30 per cent. of the insects dying during post-embryonic growth under apparently good environmental conditions are not understood. Cannibalism during the final ecdysis was observed in overcrowded and underfed cultures, but those referred to in this work were not in this condition. Although starvation due to the absence of food can be ruled out as a cause of death in these cultures, experiments were performed to measure its gross effects under differing environmental conditions.

Adults were reared in the insectary and transferred to the appropriate temperatures and humidities within 6–8 hours of the final ecdysis. Ten adults were used in each sample, and one sample of each sex, for each of the following conditions: 30°C. and relative humidities of 20, 40, 60, 80 and about 100 per cent., each being held to ± 3 per cent. throughout the experiment; and a relative humidity of 60 per cent. and temperatures of 15, 20, 25, 30, 35 and 40°C., controlled to ± 0·25°C. Each insect was weighed at the beginning of the

TABLE VIII.

Water loss from adults of *D. fasciatus* starved at 30°C. and differing relative humidities. Weights are expressed as percentages of the initial fresh weights. Each figure is the mean of 20 observations.

	Sex	Relative humidity (%)				
		20	40	60	80	100
A. Length of life in days	♂♂	3·1	3·35	3·95	4·6	4·95
	♀♀	3·6	4·05	3·7	4·85	6·3
B. Fresh weight at death	♂♂	57·2	57·1	62·0	65·3	59·8
	♀♀	61·5	72·6	64·1	63·7	56·2
C. Dry weight at death	♂♂	25·2	23·8	24·7	27·9	21·4
	♀♀	24·0	26·2	20·1	23·8	20·0
D. Water content at start of experiment (100–C)*	♂♂	74·8	76·2	75·3	72·1	78·6
	♀♀	76·0	73·8	79·9	76·2	80·0
E. Water content at death (B–C) ..	♂♂	32·0	33·3	37·3	37·4	38·4
	♀♀	37·5	46·4	44·0	39·9	36·2
F. Rate of water loss per day $\left(\frac{D-E}{A}\right)$	♂♂	13·8	12·8	9·6	7·5	8·1
	♀♀	10·7	6·8	9·7	7·5	6·9

* This assumes that there is no loss of dry weight during the experiment.

TABLE IX.

Water loss from adults of *D. fasciatus* starved at different temperatures and 60% R.H. Weights are expressed as percentages of the initial fresh weights. Each figure is the mean of 20 observations.

	Sex	Temperature (°C.)					
		15	20	25	30	35	40
A. Length of life (days) ..	♂♂	9·86	5·3	4·4	3·9	2·3	0·5
	♀♀	11·0	6·4	5·6	3·7	3·3	0·9
B. Fresh weight at death ..	♂♂	61·6	71·4	56·0	61·9	59·5	68·8
	♀♀	59·9	67·3	59·7	56·0	61·7	74·3
C. Dry weight at death ..	♂♂	24·1	23·5	23·6	24·6	25·6	28·0
	♀♀	22·8	22·2	22·8	20·6	24·4	28·3
D. Water content at start of experiment (100–C)* ..	♂♂	75·8	76·6	76·0	75·3	74·3	71·9
	♀♀	77·1	77·7	77·2	79·4	75·6	71·7
E. Water content at death (B–C)	♂♂	37·5	47·9	32·4	37·3	33·9	40·8
	♀♀	37·1	45·1	36·9	35·4	37·3	46·0
F. Rate of water loss per day $\left(\frac{D-E}{A}\right)$	♂♂	3·9	5·4	9·9	9·7	17·6	62·2
	♀♀	3·6	5·1	7·2	11·9	11·6	29·6

* This assumes that there is no loss of dry weight during the experiment.

experiment and at 24-hour intervals until it died. The length of life and the fresh and dry weights at death were recorded. These results are given in Tables VIII and IX.

The survival period of starved adults decreases with increasing temperature, the females generally living longer than the males (fig. 5). Observations showed

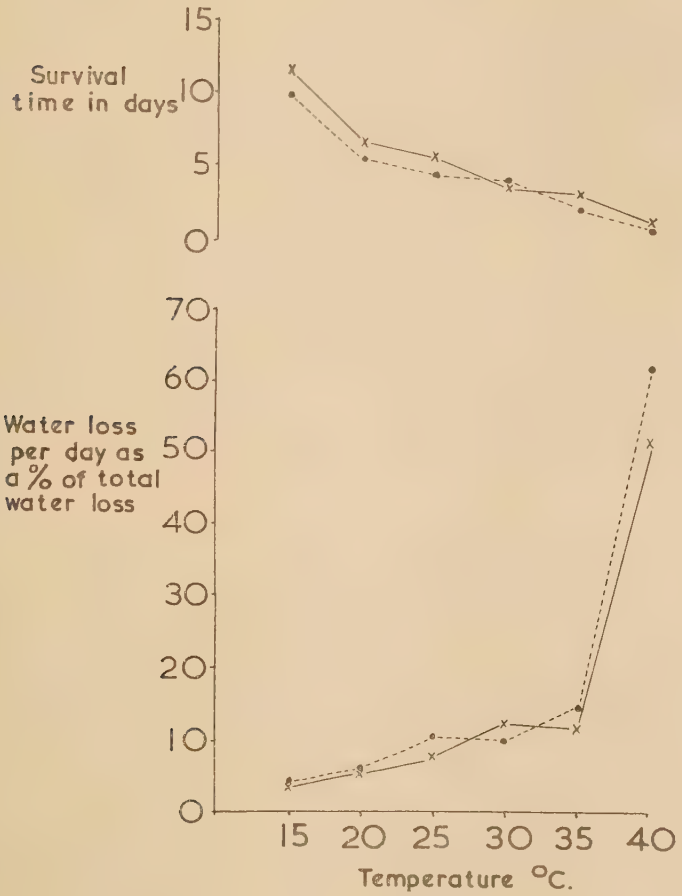


Fig. 5.—The survival time in days, and the water loss per day, of starved adults of *Dysdercus fasciatus* reared at 28°C. and placed at the appropriate temperature within 6–8 hours of their final ecdysis. ● - - - ●, male; x——x, female.

that the adults did not feed between the last ecdysis and the commencement of their forced starvation, so that much of the loss of weight under these conditions would have been due to water loss. On this assumption, the rate of water loss at different temperatures can be calculated from the data given in Tables VIII–IX. The results are shown in fig. 5, which is a typical water-loss/temperature curve.

Similar results obtained for different constant humidities at the same temperature are shown in fig. 6. Both males and females show some ability to restrict

water loss at low humidities, while at high relative humidities (above 80 per cent.), the male shows no decrease in water loss but the female does.

As might be expected, the death of the animal due to starvation is hastened by high temperatures and low humidities. The female is better able to withstand these conditions than is the male, probably because of her larger size.

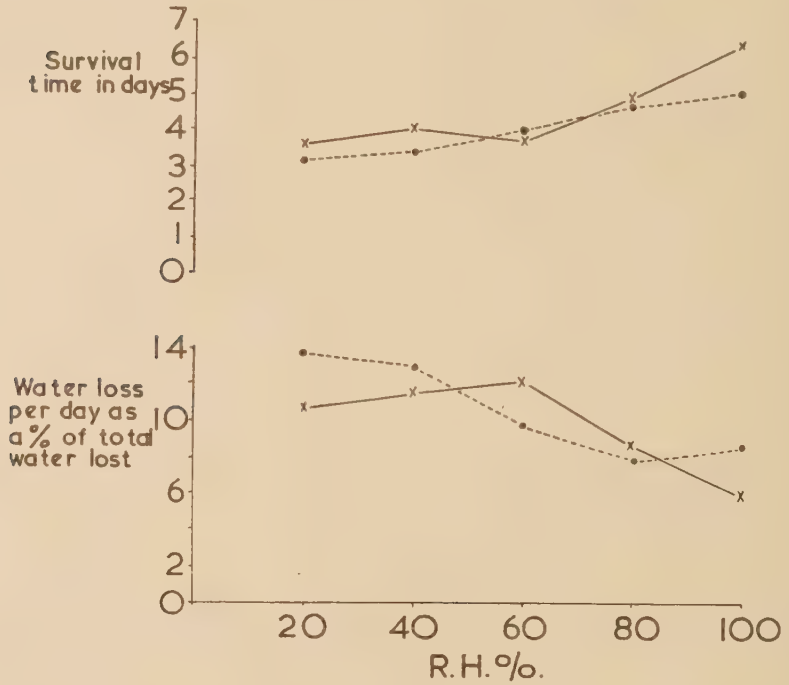


Fig. 6.—The survival time in days, and the water loss per day, of starved adults of *Dysdercus fasciatus* reared at 28°C. and 70 per cent. relative humidity and placed in the appropriate relative humidity within 6–8 hours of their final ecdysis. ● · · · ●, male; x——x, female.

Reproduction.

The average live weight of the adult female immediately after the last ecdysis is 100·2 mg. and of the male 54·6 mg. In the adult male, the weight does not greatly increase during life, but fluctuates between 83 and 119 per cent. of the initial weight. The female, however, shows an increase of 60–80 per cent. of her initial weight, due mainly to the growth of the ovaries. For 20 females dissected on the first day of adult life, the mean fresh weight of the ovaries was 7·2 mg. and of the carcass 92·8 mg. For 20 individuals on the fourth day, these weights were 50·1 and 108·8 mg., respectively, showing an increase of 42·9 mg. for the ovaries and 16·0 mg. for the carcass. It is therefore reasonable to accept this increase in the weight of the female as evidence of ovarian development and to follow the effect of temperature upon this by recording the increase in live weight of females.

Results are shown in fig. 7; each curve refers to one individual and is typical as judged by comparison with graphs prepared for each of the ten females measured at each temperature tested.

At 15°C., there was very slow growth of the ovaries, which reach a maximum weight in 24 days, but judging from their appearance, full growth was not obtained before the animal died, and no eggs were laid at this temperature. At 20°C., growth was more vigorous and a few eggs were laid, but full development was only reached at 25 and 30°C. At these temperatures, loss of weight due to

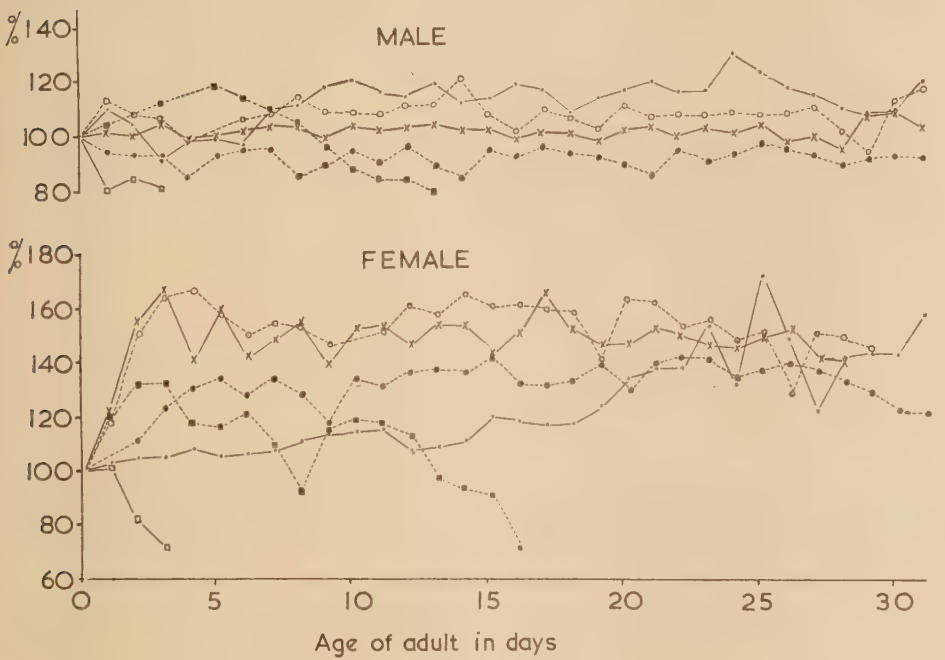


Fig. 7.—The change in fresh weight of adults of *Dysdercus fasciatus* kept at different constant temperatures. Each curve refers to one individual and the weight is expressed as a percentage of the weight of the insect immediately after its final ecdysis. ·——·, 15°C.; ●- - -●, 20°C.; o- - -o, 25°C.; x——x, 30°C.; ■- - -■, 35°C.; □——□, 40°C. For temperatures 15, 35 and 40°C., at which post-embryonic growth was not complete, the curves refer to individuals reared at 28°C. and placed in the appropriate temperature within 6–8 hours of their final ecdysis.

egg deposition did not always show up as a change in live weight, because the female sometimes fed between successive weighings. At 35°C., there was less growth of the ovaries, although some eggs were laid, and at 40°C. the female lost weight and the ovaries did not mature.

The male did not show such a well defined reaction to temperature and, although it had a shorter life span at 35°C. than at lower temperatures, it was still able to fertilise females upon the last day of its life at this temperature.

The female lays its eggs in batches; at 28°C., the first batch is laid on the fourth day of adult life and successive batches thereafter at approximately 3-day intervals. Six batches was the maximum laid by a single female. Most females died before laying this number, but several survived the laying of the sixth batch by intervals longer than their interoviposition periods.

At 28°C., the adults usually started to copulate upon the second day of the adult female's life; the males emerged about 24 hours ahead of the females from the same batch of eggs. Copulation occurred after each batch of eggs had been

deposited; it did not take place at 15 or 40°C., but at intermediate temperatures the time spent in copulation was a minimum at about 25°C. (see Table X).

The number of eggs laid by the female may be related to its absolute size; small ones, produced by restricting supplies of drinking water during development,

TABLE X.

The effect of temperature on some aspects of reproduction (time in days).

	Temperature (°C.)			
	20	25	30	35
Precopulation period	6·0	2·0	1·5	1·0
Preoviposition period	14·0	7·3	4·6	6·6
Length of life of female	38·3	20·7	21·9	21·7
Time spent in copulation	26·3	6·9	9·0	12·4
Percentage of females that laid eggs	30	80	90	80
No. of egg-batches per laying female	1·7	2·25	3·1	1·4

lay fewer eggs than larger ones whose development has not been restricted (see Table XI). Further work on the effect of the environment on fecundity refers to insects whose weights fell within the range of the heavier group of males and females.

Detailed studies were carried out to see if there was any difference in the number of eggs in, and hatchability of, successive batches of eggs obtained from

TABLE XI.

Relationship between egg-production and weight of adult. Figures given are for samples of 20 pairs.

Weight (mg.)				No. of egg-batches per female	No. of eggs per batch
Male		Female			
Mean	Range	Mean	Range		
40·9	30·1–51·6	68·7	62·6– 76·6	3·9	47·8
54·6	47·6–66·4	100·2	75·8–117·3	3·75	80·4

the same female. Twenty pairs of males and females were kept isolated under insectary conditions and the eggs laid daily were counted, incubated at 28°C. and the nymphs counted within six hours of their hatching. Results were subjected to an analysis of variance, the variance between batches having the same batch number being compared with that between successive batch numbers. There was no significant difference between the first five batches as regards their size,

but this differed significantly from that of the sixth batch, which contained only just over half the number of eggs usually found in the former. The hatchability of the last batch was found to be significantly less than that of the others, of which the first was significantly the lowest. It may be recalled that at 30°C. the third adult age-group makes the greatest contribution to r and that this corresponds in time to the appearance of the second batch of eggs, which is usually laid 7–9 days after the final moult. The above differences were all significant at the 1 per cent. level.

The effect of temperature upon some of the aspects of reproduction discussed above is shown in Table X.

The Unmated Female.

During the course of the work, a number of observations were made on isolated virgin females. Not only did their eggs prove sterile, as expected, but they also differed in a number of other respects from mated females (Table XII).

TABLE XII.

Differences between mated and unmated females of *D. fasciatus* at 28°C. and 70 per cent. R.H. Each figure represents the mean of observations on 20 females. Time in days.

	Mated	Unmated
Length of life	18·05	38·75
Preoviposition period	5–6	5–6
Interoviposition period	3·5	9·5
No. of egg-batches per female	3·75	1·8
No. of eggs per batch	80·4	73·3
Percentage of females observed to lay eggs ..	100	20

At 28°C., the mean duration of life of the virgin female is twice that of the mated female, her interoviposition period is about three times as long, and she produces only about half as many egg-batches, although the number of eggs per batch is nearly the same as in the mated female.

At 35°C., the duration of life of the mated and unmated female is nearly the same, and only the first batch of eggs is developed. In the mated female this batch is laid, but in the unmated female it is retained and reabsorbed. This process has been followed by weighing the ovary in batches of 10 females, killed and examined at daily intervals, and followed by histological examination (fig. 8 and Pl. IX). On the first day, the ovaries (Pl. IX, fig. 1), as might be expected, did not differ from those of females kept at lower temperatures or of mated females at 35°C. No difference was detected between the ovaries of these groups on the fourth day (Pl. IX, fig. 2). By the ninth day, the ovaries of the unmated females kept at 35°C. had shrunk and assumed a characteristic appearance. The two ova were lying side by side in the follicle (Pl. IX, fig. 3), instead of one above the other, and the accessory membrane had started to thicken. By the 14th day (Pl. IX, fig. 4), the ovum was invaded by epithelial cells derived from the follicular epithelium (phagocytes do not seem to have been involved), which

absorbed the yolk, particles of which became visible in the cytoplasm of the invading cells (Pl. IX, fig. 5). The accessory membrane was greatly thickened and had a striated appearance.

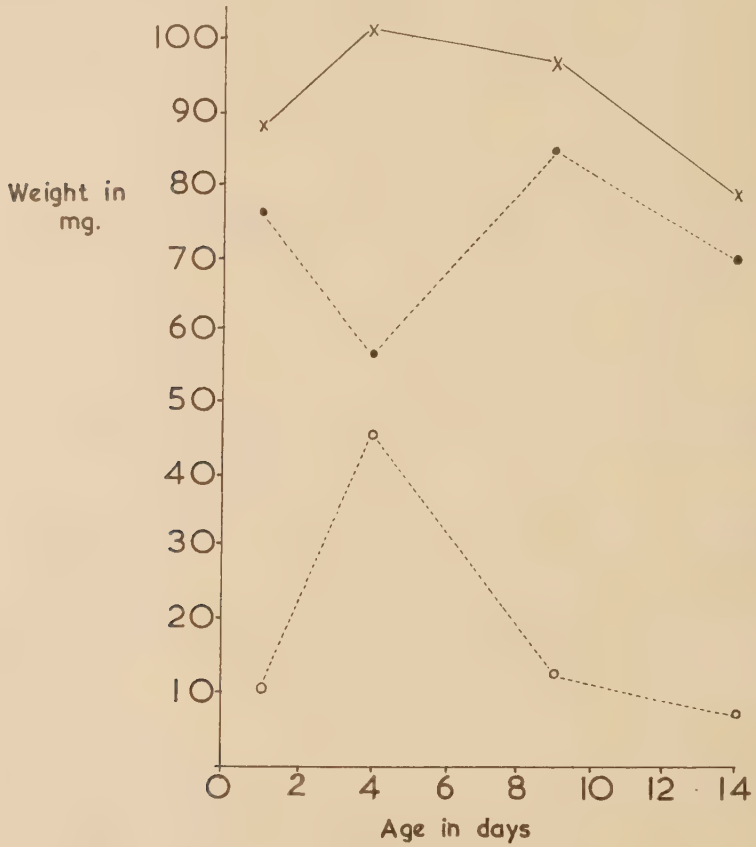


Fig. 8.—The relationship between fresh weight of ovary and cascass, and time, during the adult stadium of unmated females of *Dysdercus fasciatus* kept at 35°C. o - - - o, weight of ovary; ● - - - ●, weight of carcass; x——x, weight of ovary + carcass. Each point represents the mean weight of a sample from 20 individuals.

Discussion.

The data obtained in these studies on the biology of *D. fasciatus* are, in the main, in good agreement with published records for this and other species of the genus.

The calculated threshold of development of the egg was 5°C., but as only two points were available it cannot be regarded as a very reliable estimate, and is lower than that given by other workers with *Dysdercus*. In the conditions of the present experiments, eggs did not develop at all at 15°C. and none hatched at 20°C., although the embryo developed to the stage at which an orange pigment was deposited. At the other end of the temperature scale (35°C.), none passed

this stage of development. The causes of death at temperatures below 25°C. and the reasons for the discrepancy between the calculated and observed threshold of development are being further studied in this laboratory.

The results obtained in calculating the intrinsic rate of increase (in the limited sense in which that has been considered here) are comparable amongst themselves. They do not represent true values for the population, since mortality in the egg stage has not been taken into account; the values for r are thus too high. In *D. fasciatus*, the value of r increased 3·56 times for a rise of 10°C. (from 20 to 30°C.); in *Ptinus tectus* Boield. it increases 2·6 times for a rise of 10°C. (from 15 to 25°C.) (calculated from data given by Howe, 1953).

Table I, which shows a considerable shortening of the life-cycle with increasing temperature, supports the conclusion of Birch (1948) and Howe (1953) that this is one of the major effects of temperature upon r. The importance of this in *D. fasciatus* is obvious, but the analysis shows that other factors are of nearly equal or greater importance. Thus, the effect of temperature upon the number of batches of eggs laid per female is such that at 30°C. almost twice as many (3·1) are laid as at 20°C. (1·7). In any population, the percentage of females that lay eggs differs greatly according to temperature; at 20°C. only 30 per cent. of the females laid eggs, while at 30°C., 90 per cent. did so. Studies of the survival curves given in fig. 1 show that pre-reproductive mortality is affected by temperature and this too will affect the value of r. In *D. fasciatus*, then, the effect of temperature upon r is mediated through several channels, the most important of which are the length of the life-cycle, the reproductive capacity and the pre-adult mortality.

It has been shown that the number of eggs produced depends upon the size of the adult. Although different temperatures produce differences in the size of the adult, these are not as large as those produced by restriction of the water supply during growth. Moist warm conditions accordingly give rise to higher values of r than do warm dry ones.

As was pointed out at the start of this paper, the restricted meaning here given to the intrinsic rate of increase was thought to be justified, since it sums up in a single figure the total effects of environmental conditions upon a population of insects. Its application is limited to environments in which growth and reproduction can take place, but it is just within this range of conditions that an objective measure of success is hardest to obtain. Its use also encourages thought on the effects, upon a population of animals, of an environment that changes with time, rather than on comparisons between fixed points in a life-history. Whilst this may be of small importance when the effects of constant environmental conditions are being considered, it is essential when varying conditions are being studied.

For these reasons, together with the fact that in many insects the different stages pass their lives in quite different environments, it is thought that the limited meaning given to the intrinsic rate of increase in these studies might be widely applicable in laboratory studies on the growth of insect populations.

Summary.

In laboratory studies of *Dysdercus fasciatus* Sign., populations were exposed to constant temperatures of 15, 20, 25, 30, 35 and 40°C. and a relative humidity of 60 per cent., and to 28°C. and 70 per cent. R.H. After hatching, the insects were supplied with cotton seed as food and water to drink. Development of eggs was incomplete below 25°C., of nymphs below 20°C., and of both above 30°C. To allow comparison of growth and rate of reproduction at temperatures outside the embryonic range, this stage was ignored in calculating values of the intrinsic rate of increase, r, and the mortality rate and length of life were measured from

the time of hatching, the eggs being incubated under optimum conditions (those at 28°C.) and the freshly hatched nymphs then moved to the appropriate temperature. The value of r was found to increase with increasing temperatures up to 30°C., and to do so more rapidly between 25 and 28°C. than between 20 and 25°C. The age-schedule of deaths for populations living at 28°C. showed a distribution of deaths that was almost ideal, in that their highest frequency did not occur until the reproductive period was advanced. The principal deviation from this ideal was due to the high mortality rate found in the first instar. At 20°C., the death rate approached constancy throughout the life-span of the population. The interval between generations decreased with increasing temperature, the rate of decrease being approximately 4·6 days per 1°C. rise in temperature.

Further analysis of r was made by considering separately the growth and reproductive characteristics of the insect, and the effect of temperature upon them.

The rate of post-embryonic growth, as measured by live weight, increased with temperature, within the range of 20–30°C. At 15°C., growth did not proceed beyond the third instar, or beyond the fifth instar at 35°C. The principal cause of the increase in growth rate was the decrease and eventual disappearance of the periods between initial ecdysis and start of growth, and between the end of growth and final ecdysis, the rate at which growth actually took place differing but slightly.

The size of the insect just after the final ecdysis had an important effect on r because the number of eggs laid by small insects (mean weight 68·6 mg.) was only about half that of large ones (mean weight 100·2 mg.). Any decrease in size observed with increasing temperature was slight compared with that produced by restricting the insect's access to drinking water.

Copulation and oviposition occurred in adults maintained at any of the temperatures except 15 and 40°C. The percentage of females that laid eggs differed according to the temperature, the highest recorded being 90 per cent. at 28°C. and the lowest 30 per cent. at 20°C. The total time spent in copulation also varied with temperature, being least (9 days) at 28°C. and most (26·3 days) at 20°C. The change of weight of the female after moulting largely represented growth of the ovaries; at 15°C., this is slow and not completed before the female dies; at 40°C. the ovaries do not mature; at other temperatures tested (20–35°C.) growth is fairly rapid, the ovary being full grown in about four days.

The fertile female lays her eggs in batches, the maximum observed being six batches, at approximately three-day intervals. A few females survived the laying of the sixth batch of eggs by a period longer than their interoviposition period. At 28°C., the preoviposition period and the time spent in copulation were less, more egg-batches, and hence more eggs, were produced and a higher proportion of females mated, than at any other temperature. In the unmated female, the average life was twice that of the mated one, the preoviposition period was the same, the interoviposition period approximately three times as long, the egg-batches half as numerous, and the number of eggs per batch nearly the same. All fertile females were observed to lay eggs, but only 20 per cent. of the unmated ones did so. At 35°C., mated females produced one or two batches of eggs; unmated ones produced none, and although the ovary matured normally up to the fourth day, the yolk was subsequently reabsorbed, this process being complete by the 14th day.

These studies have indicated that in *D. fasciatus* the decrease in the value of r with decreasing temperature is caused by a rise in pre-reproductive mortality and a fall in reproductive capacity, as well as by the increase of the generation length, which other workers have found to be of predominating importance in the case of other insects.

References.

BIRCH, L. C. (1948). The intrinsic rate of natural increase of an insect population.—*J. Anim. Ecol.* **17** pp. 15–26.

CHAMBERS, E. G. (1945). Statistical calculating for beginners.—Camb.Univ.Pr.

DEEVEY JR., E. S. (1947). Life tables for natural populations of animals.—*Quart. Rev. Biol.* **22** pp. 283–314.

HOWE, R. W. (1953). Studies on beetles of the family Ptinidae. VIII. The intrinsic rate of increase of some Ptinid beetles.—*Ann. appl. Biol.* **40** pp. 121–133.

POMEROY, A. W. J. & GOLDING, F. D. (1923). Observations on the life histories of the cotton-stainer bugs of the genus *Dysdercus*, and on their economic importance in the Southern Provinces of Nigeria.—*2nd Annu. Bull. Dep. Agric.* Nigeria pp. 23–58.

© Commonwealth Agricultural Bureaux, 1959.



FIG. 1.

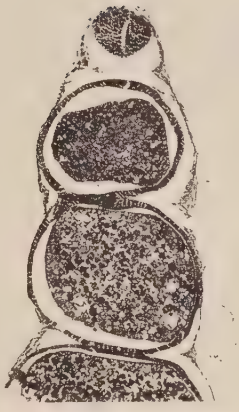


FIG. 2.



FIG. 3.



FIG. 4.

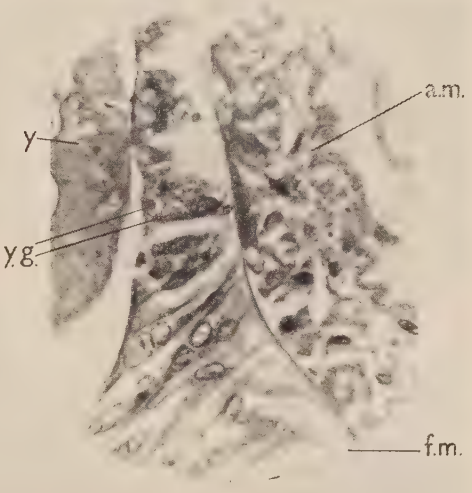


FIG. 5.

FIGS. 1—5. 1. General appearance of the ovarioles on first day of adult life (× 60). 2. Longitudinal section through an ovariole on the 4th day, showing fully matured ova lying one above the other (× 60). 3. Longitudinal section of an ovariole on the 9th day, showing eggs lying side by side instead of above one another (× 60). 4. Longitudinal section of ovarioles on the 14th day, showing invasion of egg by follicular cells and thickening of the accessory membrane (× 60). 5. Ovariole as in fig. 4 but of higher magnification (× 520), showing resorbed yolk granules in the follicular cells and thickened accessory membrane. a.m., accessory membrane; o.l.m., outer limiting membrane; f.m., follicular membrane; f.e., follicular epithelium; y., yolk; y.g., yolk granules. (For further explanation see text.)

HISTOLOGY OF THE OVARY OF AN UNMATED FEMALE OF *DYSDERCUS FASCIATUS*, KEPT AT 35° C.

STUDIES ON THE DERMESTID BEETLE, *TROGODERMA GRANARIUM* EVERTS. II.—THE OCCURRENCE OF DIAPAUSE LARVAE AT A CONSTANT TEMPERATURE, AND THEIR BEHAVIOUR.

By H. D. Burges, Ph.D.

The khapra beetle, *Trogoderma granarium* Everts, is a serious pest of stored malt in Britain and of many foods in the tropics. In infested maltings, large numbers of the insects can be found in crevices in the fabric of the stores, where they have been observed to remain for several years. Since these hidden insects are protected from the normal cleaning of the malt stores they are a very important source of infestation in new bulk malt, with the result that this species has become a particularly persistent pest.

The purpose of the present work is to study the movement of the insects in and out of crevices. The conditions of temperature and humidity in a malt store often change rapidly and irregularly, therefore the behaviour of the insects was studied in the maltings only very broadly and a detailed investigation was made in laboratory conditions. The laboratory work described in this paper is limited to that at 30°C., and studies on the effect of changing temperature will be published in a later paper.

Information from Malt Stores.

Insects were collected from the fabric of malt stores and also from pieces of corrugated cardboard left in the stores as traps. Some examples of the numbers of each stage found are given in Table I. The most abundant stages were larvae

TABLE I.

The developmental stages of *T. granarium* found in crevices and traps in malt stores.

Type of store	Position of insects	Larvae	Pupae and adults in larval skins	Free live adults	Free dead adults
Shallow bin	Under bubble of white-wash on kiln wall	13	0	0	0
Hot-air chamber	In crevices and under bubbles of ceiling and stack	235	0	0	0
	Wooden floor	52	1	1	7
Loft above a silo	In crevices in floor and roof	169	1	0	7
	Traps on same	2998	0	0	0
Loft and hot-air chamber	In traps on malt for 56 days	1877	34	2	1
	In traps on malt for 26 days	2182	21	2	7
	In traps on malt for 51 days	2517	97	45	0

in the fourth or later instars. No younger larvae were found. The method of recognising the four or more larval instars is given by Burges (1957). The presence of a few pupae and young adults not yet emerged from the last larval skins shows that the crevices are sometimes used as a site for pupation. Some samples, not included in Table I, consisted entirely of larval skins, dead adults and dead larvae, showing that some adults enter the crevices and die there.

Laboratory Populations in Cultures.

Conditions.

All the experimental cultures were kept at 30°C. and 65 to 70 per cent. relative humidity maintained in a breeding room. Continuous records show that the average temperatures during the experiments varied between 29·5 and 30·5°C. and occasionally temperatures as low as 29·0° or as high as 30·8°C. were recorded for longer than four hours, but less than 24 hours.

Wheatfeed alone or a mixture of wheatfeed and Manitoba wheat (1 : 20 by weight) were used as foods. Wheatfeed contains fine bran and some endosperm. It was included in the mixture because young larvae are believed to have some difficulty in attacking sound wheat grains.

Design of standard experimental crevices.

Observations in maltings had shown that the insects entered cracks in all building materials and that narrow spaces were filled before wide ones. Bearing this in mind, some laboratory experiments were devoted to the design of a suitable crevice for use in cultures.

To discover the best width of crevice, batteries of crevices were put into cultures (fig. 1, left). The batteries were made by clipping together small, thin blocks of planed wood with elastic bands, then inserting pieces of glass slide and

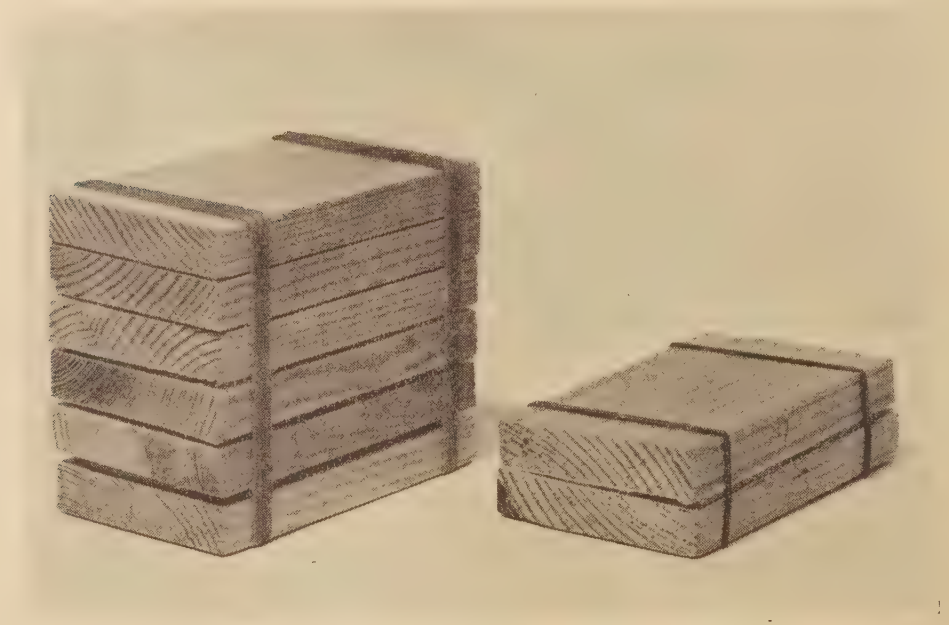


Fig. 1.—Left, battery of crevices; right, standard crevice.

mica of different thicknesses between the blocks to form fissures of even but different width. Spaces about 1·2 mm. wide were preferred by the larvae in these experiments (fig. 2). A series of experiments was carried out to find better

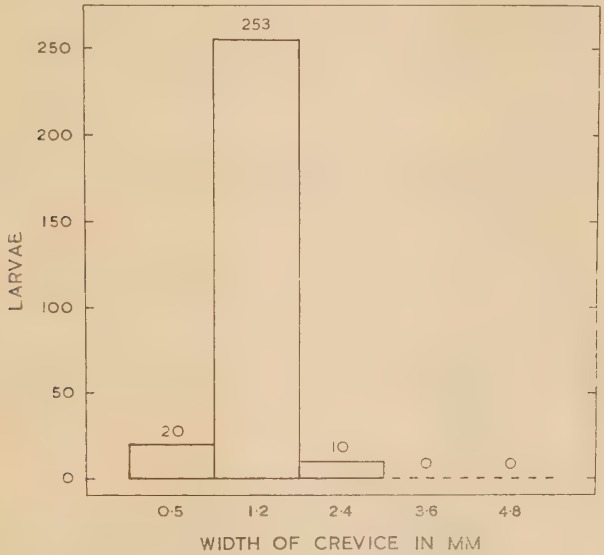


Fig. 2.—The numbers of larvae of *T. granarium* found in wooden crevices left for two days in a culture. Two replicate experiments have been combined.

materials than wood for making the crevices. When the wood was replaced by a transparent material, perspex, no larvae entered the crevices, probably due to the slippery nature of perspex. Crevices with very rough surfaces were made by sticking either hessian sack cloth or cotton cambric over the wood. Large numbers of larvae accumulated in these crevices, but they did not prefer them consistently to crevices made with uncovered wood.

The experience gained in these experiments was incorporated in the design of the standard crevices to be used in all subsequent experiments. Instead of batteries of crevices, which were clumsy to handle, a large number of exactly replicated single crevices were made (fig. 1, right). Each single crevice consisted of two blocks of wood, 4·5 × 7·5 × 0·9 cm., clipped together with elastic bands and held apart along one side only by a narrow strip of cardboard. The cardboard was 1·6 mm. thick and 7 cm. long. The crevice space formed was triangular in cross section, providing a space of varying width suitable for insects of variable size. To form a standard rough surface of even texture and not retaining the odour of the cement, cotton cambric was stuck over the inner surfaces of the wooden blocks with a cellulose-acetate cement. Crevices of the above size were used in cultures in jam jars. For smaller cultures in 3 × 1-in. glass specimen tubes, a large number of small crevices were made to the same design, using cardboard instead of wood. The pieces of cardboard were 2 × 5 × 0·16 cm. in size and they were lined with cotton cambric.

Development and behaviour of insects in cultures.

The movement of insects into crevices at different developmental stages was studied in many cultures.

One of these cultures was started with 128 newly-hatched larvae placed on 4·2 g. of the mixture of wheat and wheatfeed in a 3 × 1-in. specimen tube. A small crevice was stood gently on top of the food. The crevice was lifted out of the tube for examination every one or two days, and the food was examined every four or five days; all pupae were removed to prevent the development of a second generation.

The results are illustrated in fig. 3. On the 20th day after hatching, two

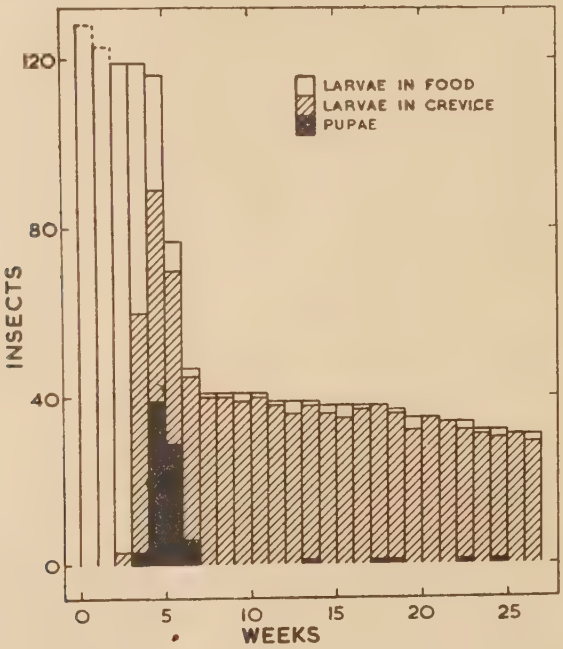


Fig. 3.—The development and behaviour of larvae of *T. granarium* in a culture containing a crevice. The histograms illustrate the numbers of larvae in the food and in the crevice at the end of each week after hatching, also the number of pupae found and removed during each week. Nine larvae died in the first two weeks and six in the next 25 weeks.

larvae appeared in the crevice and thereafter the number increased steadily. Most of these larvae were in their fourth or in a later instar, although a few may have been in their third instar. Many cast larval skins were found in the crevice and occasionally the number of larvae in the crevice fell slightly, suggesting that possibly some individuals left the crevice after moulting. On the 26th day, the first pupa appeared in the crevice and subsequently the numbers of pupae found in both the crevice and the food increased rapidly to a maximum and then decreased (fig. 3). These insects developed in a similar time to insects bred in isolation, the females taking slightly longer than the males (Burges, 1957).

After seven weeks, 41 large larvae were left, and pupation ceased except for an occasional individual. At each observation, most of these larvae were found in the crevice, suggesting that they spent most of their time there (fig. 3). The larvae in the crevices clustered together very closely. When the sides of the crevice were held apart, no larvae moved for a short while, then a few began to wander. On one occasion the crevice in another culture was kept open much longer than usual and many larvae were still immobile after five minutes, indicating that in the crevices larvae lapse into a very inactive state. Apart

from their different behaviour and their delayed pupation, these larvae appear to be similar to those which pupate in a normal time. In this paper, these long-lived, inactive larvae are termed diapause larvae, in contrast to the others with a short developmental period, which are termed normal. The only means of distinguishing the two types of larvae appear to be the aggregation of diapause individuals in crevices combined with delayed pupation, usually recognisable after seven weeks at 30°C.

In another culture, the pupae were not removed and a second generation of larvae developed, which did not enter the crevice until the fourth instar (with possibly a few individuals in the third instar).

The combined results of 82 cultures showed a 1 : 1 sex ratio (1,788 males to 1,770 females). Among the normal insects, the males predominated slightly (60% males) and there were correspondingly more females (56%) among the diapause insects.

The effect of disturbance.

Two large cultures in 7-lb. jam jars were used to find the effects of disturbance. The crevices were examined daily, but otherwise the cultures were similar to that referred to in fig. 3. The results are given in Table II. In culture A, great care was taken not to disturb the food until it was sieved after 47 days. In culture B, the food was stirred with the hand on the 23rd day. Next day, many larvae were found in the crevices in culture B, but none were found in those of culture A.

TABLE II.

The behaviour of *T. granarium* in cultures. The values are percentages of the total insects of the first generation found in the culture on the 47th day.

Days after eggs laid	Remarks	Culture A (980 insects) : food not handled		Culture B (631 insects) : food handled on day 23	
		Crevices	Food	Crevices	Food
8	Crevices put in ..	—	—	—	—
9–22	Food untouched ..	0	all	0	all
23	Food stirred in B only	0	all	0	all
24	Food untouched ..	0	all	17·4L	rest
25	Food untouched ..	—	—	—	—
26	Food untouched ..	2·0L	rest	32·0L 0·3P	rest
27	Food untouched ..	4·7L 0·8P	rest	23·1L 1·1P	rest
47	A and B, food sieved, crevices opened ..	23·5L 0 P 27·6A	1·9L 0·3P 46·6A	53·2L 0 P 31·2A	0·3L 0·6P 14·6A
Total insects in each stage after 47 days :		25·4L 0·3P 74·3A 100 all stages		53·6L 0·6P 45·8A 100 all stages	

L, large larva; P, pupa; A, adult.

Also, on the 26th and 27th days, there were more larvae in the crevices in the disturbed than in the undisturbed culture. This indicates that disturbance of the food encourages the larvae to enter the crevices, an effect often noticed subsequently in other cultures.

Behaviour of Diapause Larvae.

After counting all the insects in the two cultures A and B on the 47th day, the diapause larvae aggregated in three crevices were used for further long-term observations. All the adults, pupae and larval skins were cleared from these crevices without removing the larvae, then each crevice was placed in a fresh jar on new wheat. Thereafter the food was sieved at intervals and the larvae found in it were returned, but pupae and adults were discarded. The three crevices contained 45, 113 and 196 larvae, respectively, but since the three cultures were not always examined on the same day, the three sets of results could not be compounded, although they were very similar, and those of the largest only are illustrated in fig. 4.

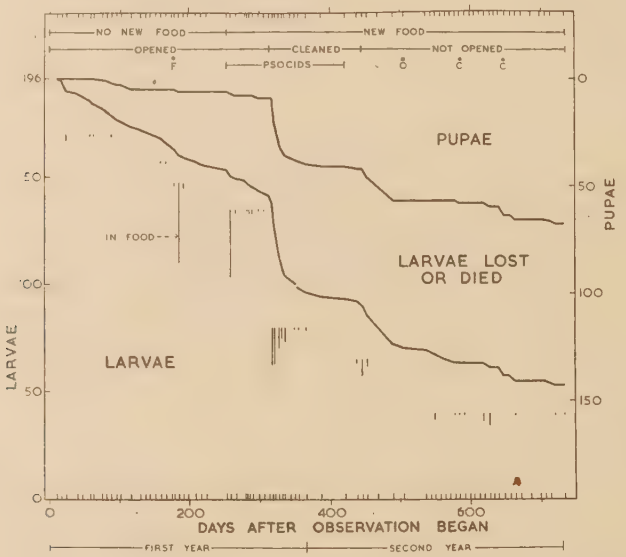


Fig. 4.—The behaviour of diapause larvae of *T. granarium* in a culture with a crevice, at constant conditions. The food in the culture was sieved at intervals shown by the small lines on the abscissa. Various aspects of the experimental technique are shown at the top of the diagram.

In the figure, the number of larvae remaining in the culture is shown by the lower curve. The cumulative number of pupae is plotted on an inverted scale in the upper curve. Some larvae died and their bodies were found; others disappeared without trace, suggesting that some cannibalism or eating of dead bodies took place, or that a number of larvae were lost during handling; it was known that a few larvae were lost, but losses are unlikely to account for all the missing larvae. In the figure, the combined deaths and losses are represented by the space between the upper and lower curves. For example, by the 490th day, 72 larvae remained in the culture (lower curve), 57 had pupated (upper curve) and 67 had died or were lost (space between the two curves). The upper curve

in fig. 4 illustrates the very low rate of pupation. In Table III the results of all three cultures have been combined showing that only a quarter of the larvae pupated in the first year and that one sixth of the larvae had still not pupated in four years. In contrast, normal larvae pupate in 29 to 44 days after the eggs are laid (Burges, 1957).

The larvae moulted occasionally both in the food and in the crevices, skins gradually accumulating in the crevices.

Sporadically, larvae were observed in the food, usually in very small numbers. These larvae are indicated in fig. 4 by vertical lines drawn below the lower curve

TABLE III.

The pupation of diapause larvae of *T. granarium* given crevices in three cultures.

	One year	Two years	Four years
Pupae	84 (24%)	128 (36%)	150 (42%)
Larvae lost or died ..	97 (27%)	130 (37%)	149 (42%)
Larvae remaining ..	173 (49%)	96 (27%)	55 (16%)
Total insects	354	354	354

representing total larvae, so that the rest of the distance between this curve and the base line indicates the larvae in the crevice. For instance, when the food was sieved on the 24th day, 3 larvae were found in the food out of a total of 190, leaving 187 in the crevice. There is no suggestion of rhythmical behaviour, although on a few occasions a distinct increase in the number of larvae appearing in the food could not be associated with a change in the experimental technique, *e.g.*, that on the 445th day. Initially the food was not renewed and the crevices were opened just long enough to remove any adults and pupae at each observation, as shown along the top of the figure. On the 252nd day, an infestation of Psocids was found in the cultures and two changes in the technique were made to eliminate these intruders: 1. the food was renewed at every sieving without disturbing the larvae in the crevices more than usual, 2. nine weeks later the crevices were cleaned regularly for 18 weeks by removing the skins and Psocids from them. At the beginning of each of these treatments the number of larvae found in the food increased markedly, then decreased again in spite of the continuance of the treatments. The quantities of frass changed similarly, showing that many of the larvae fed. There is no evidence that the Psocids themselves had any effect on the larvae. Regular treatments are shown by the lines along the top of fig. 4 and isolated departures from these treatments are shown by letters: F indicating new food without extra disturbance of the larvae in the crevice, C indicating that the crevice had been cleaned and O indicating that the crevice had been opened just long enough to count the larvae inside. Sometimes these isolated treatments were followed by an increase of the larvae in the food, *e.g.*, on the 185th day. Sometimes a large increase in the numbers of larvae in the food was followed by an increase in the number of pupae, *e.g.*, 22 per cent. of the total larvae pupated following the 252nd day in fig. 4.

It is concluded that new food given suddenly after the old food has become " stale ", and severe disturbance following a long period when the larvae had been left undisturbed, sometimes caused some larvae to emerge and feed, an effect warranting further experimental study.

Behaviour of Diapause Larvae in Crevices after Disturbance.

The behaviour of diapause larvae clustered together in crevices varied according to the degree of disturbance inflicted upon them and according to the temperature. The following observations were made at 30°C., larvae being a little more active at higher temperatures such as 35 and 40°C. and much more sluggish at temperatures near 20°C.

The position of an undisturbed group of larvae in a crevice remains very constant. For instance, only six larvae were found outside a pencil line drawn ten days earlier around a group of 45 larvae in a small crevice.

In contrast, when a crevice was left open to expose a group of larvae on each wall of the crevice, a small number of larvae that had lost their footing moved away; then gradually other larvae began to move, a few at a time, principally near the edges of the group, until eventually all the larvae dispersed. This behaviour has been observed in malt stores in both daylight and darkness.

A small number of larvae wander if a crevice is left open just long enough to count the larvae inside and to remove their cast skins. Some examples are given in Table IV. When the wandering larvae were brushed back on top of the group and the crevice was closed, only a few larvae emerged again immediately.

TABLE IV.

The behaviour of diapause larvae of *T. granarium* in a crevice when the crevice is opened briefly.

Larvae in crevice	Crevice open	Number of wandering larvae
843	5·75 min.	59 (7%)
57	1·5 min.	1 (2%)
37	0·5 min.	0

Having shown that careful handling of the crevices does not cause much movement of diapause larvae immediately, it is necessary to establish whether handling stimulates a delayed movement of larvae into the food. For this purpose, five small crevices containing larvae which had recently entered diapause were placed in a jar containing fresh wheat. The treatment of these larvae and the results are given in Table V. Every four to nine days the larvae found in the wheat were discarded and the wheat was renewed. As might be expected from fig. 4, the sudden presence of fresh food stimulated some larvae to emerge from the crevices (*e.g.*, 15% on the 20th day), after which the larvae became habituated to new food, as shown by the small numbers found in the food on the 28th and 32nd days (less than 3%). On the 32nd and again on the 38th days, the crevices were handled sufficiently to count the larvae inside and to remove the cast larval skins. For six or nine days after each disturbance, the larvae in the food were counted at intervals of increasing length without discarding them or renewing the food (Table V). The numbers of larvae found in the food remained very low and there was no evidence that the larvae were induced to leave the crevices by the disturbance. In contrast, following a comparable disturbance (cleaning of crevices on the 313th day) in the experiment illustrated in fig. 4, 18 (13%) of the larvae were found in the food. A reasonable explanation of this difference is the age of the larvae; during diapause for nearly a year (fig. 4), these

larvae presumably used some of their food reserves and they were perhaps more ready to feed than larvae which had been in diapause less than two months (Table V).

TABLE V.

The effect of severely disturbing diapause larvae of *T. granarium* in crevices at 30°C. and 70 per cent. R.H.

Day	Internal between sievings	New food	Larvae in food No.	Larvae in food %	Treatment of larvae in food
20	5 days	Yes	101	15·3	Discarded
28	8 days	Yes	11	1·9	,,
32	4 days	Yes	16	2·9	,,
	Crevices disturbed, contained approximately 533 larvae				
32	1 hr.	No	1	0·2	Replaced
32	2 hr.	No	7	1·3	,,
32	4 hr.	No	12	2·2	,,
33	17 hr.	No	17	3·2	,,
34	1 day	No	23	4·3	,,
36	2 days	No	19	3·6	,,
38	2 days	Yes	16	3·0	Discarded
	Crevices disturbed again				
38	1 hr.	No	1	0·2	Replaced
38	2 hr.	No	1	0·2	,,
38	4 hr.	No	33	6·2	,,
39	17 hr.	No	9	1·7	,,
40	1 day	No	19	3·6	,,
42	2 days	No	11	2·1	,,
47	5 days	Yes	13	2·4	Discarded
51	4 days	Yes	19	3·6	,,

Behaviour of Diapause Larvae denied a Crevice.

Diapause larvae in a culture without a crevice are in continuous contact with their food and they are subjected to severe disturbance every time the culture is examined. This treatment might prevent or break diapause, or it might affect the moulting, size and feeding of the diapause larvae. These possibilities were tested using cultures kept with and without crevices.

Initiation of diapause.

A typical pair of cultures was started by placing 128 newly hatched larvae on the mixture of wheat and wheatfeed in each of two tubes one in. wide. A small crevice was placed in one culture. Every four or five days, the crevice was opened very briefly and the food was examined thoroughly to remove skins, pupae and adults, all of which were discarded.

Many larvae pupated during the first seven weeks after hatching and none did so in the next two weeks; therefore it was assumed that all the normal larvae had pupated by the seventh week. At this time, 38 larvae remained in the culture without a crevice and 40 in the culture with one. These were regarded as diapause larvae and their presence in both cultures showed that diapause can take place whether or not a crevice is present.

Breaking of the diapause and pupation.

Regular observations were continued on these two cultures to find the effect of a crevice on the pupation of diapause larvae. The results, dating from the time

that all the normal larvae had been removed, are illustrated in fig. 5. During the first 135 days after this time, 12 per cent. of the diapause larvae with a crevice and 21 per cent. of those without one pupated. A chi-square test (Snedecor, 1938) showed that this difference was not statistically significant. Similar results were obtained in another seven pairs of cultures. In addition, a comparison of

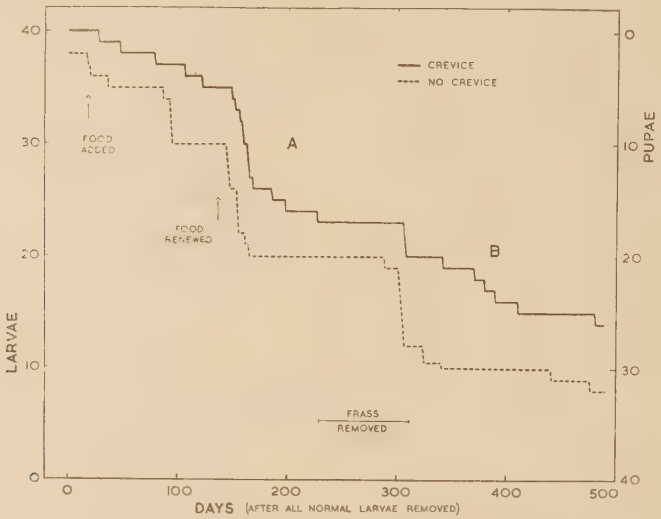


Fig. 5.—The rate of pupation in two cultures of diapause larvae of *T. granarium* with and without a crevice, respectively. The numbers of larvae remaining in the culture are given by the scale on the left; they include larvae which died or were lost during the 500 days (11 and 6, respectively). The numbers of pupae are given by the inverted scale on the right.

the two curves in fig. 5 for the whole experiment shows similar proportions of larvae pupating, despite two bursts of pupation, one at A, which followed a renewal of the food with fresh wheat after more than half of the original food had been eaten, and the other at B, which took place some time after the start of

TABLE VI.

The effect of a crevice on the amount of frass produced by diapause larvae of *T. granarium* in four pairs of cultures in two months.

Crevice present		No crevice		Ratio
Larvae in culture	Frass per larva (mg.)	Larvae in culture	Frass per larva (mg.)	(no crevice : crevice)
27	0·81	33	1·83	2·3
12	0·29	19	0·79	2·7
10	0·57	12	1·65	2·9
10	0·15	5	5·76	38·4
Combined 59	0·55	69	1·80	3·3

sieving off the frass (faecal pellets and some food fragments). The burst of pupation at B may suggest that the accumulation of frass inhibits the breaking of diapause to some extent.

Moulting, size and feeding.

In all cultures kept under observation, resting in a crevice did not noticeably affect the frequency at which diapause larvae moulted. For example, in 61 days a group of 37 larvae with a crevice underwent 1·16 moults per larva and 33 larvae without a crevice had 1·30 moults per larva.

After eight months in diapause, the average weight of 65 larvae kept in a culture without a crevice was 4·2 mg. and that of 93 kept with one was 3·2 mg.

Without a crevice, larvae produced more frass. In four pairs of cultures, the frass was weighed to the nearest 0·01 mg. (Table VI). Larvae without a crevice produced about three times as much frass as those with one. These experiments show that larvae confined to the food feed more than those allowed to rest in a crevice. This could be attributed simply to the greater proximity of the larvae to the food, but it is likely that the greater disturbance at every observation was also a controlling factor.

The bigger larvae produced bigger adults. The results of weighing the insects during the first day of adult life are given in the left half of Table VII. Diapause larvae without a crevice produced much heavier beetles than those with a crevice.

TABLE VII.

The weight (in mg.) of beetles produced by diapause and normal larvae of *T. granarium* with or without a crevice.

	Adults from diapause larvae		Adults from normal larvae		*P*
	N	M ± S.E.	N	M ± S.E.	
Crevice, females ..	14	2·56 ± 0·13	33	2·60 ± 0·09	0·60
No crevice, females ..	24	4·04 ± 0·13	39	3·02 ± 0·11	<0·05
P	<0·01		<0·05		
Crevice, males	10	1·00 ± 0·06	42	0·86 ± 0·08	0·05
No crevice, males ..	2	1·30 ± 0·00	41	0·96 ± 0·03	<0·05
P	<0·01		<0·01		

The beetles were weighed to the nearest 0·01 mg.

Some interesting comparisons can be made between the adults produced by the diapause larvae and those by the normal larvae. Without a crevice, the adults produced by diapause larvae were much heavier than those from normal larvae (Table VII). Presumably the diapause larvae assimilated more food during their extended larval periods than did normal larvae. In the presence of crevices, females of the two types were about the same size and males produced by diapause larvae were only 16 per cent. heavier than males formed by normal larvae. This suggests that diapause larvae resting in a crevice feed only sufficiently to replace the stored food used during the resting periods.

Behaviour of Diapause Larvae given Fresh Food.

Following the enforced renewal of food on the 252nd day due to infestation by Psocids, 22 per cent. of the larvae in a culture pupated (fig. 4). To decide whether this effect of new food could be repeated, the wheat in six small cultures was renewed and that in six replicates was not. During the next six weeks, only 6 per cent. of the larvae given fresh food pupated. However, when the food in two similar cultures was renewed without abnormal disturbance of the larvae in the crevices, many larvae emerged from the crevices and 36 per cent. of the 58 larvae pupated in six weeks. Thus a very variable proportion of the diapause larvae pupate after a single renewal of the food.

The long-term effect of renewing the food fortnightly was measured over nine months. Four groups of three cultures were subjected to the following four treatments respectively:—

Crevice absent, stale food.
Crevice absent, new food.
Crevice present, stale food.
Crevice present, new food.

TABLE VIII.

The long-term effect of continual new food on breaking the diapause of larvae of *T. granarium* in four groups of three cultures over nine months.

	Stale food		New food	
No crevice ..	77 larvae	7 (9%) pupae	59 larvae	21 (36%) pupae
Crevice ..	79 larvae	9 (11%) pupae	51 larvae	11 (22%) pupae

The new food increased the proportion of pupae by 27 per cent. when no crevice was available and by 11 per cent. with a crevice present (Table VIII). On applying chi-square tests, only the increase without a crevice was found to be significant ($P < 0.01$).

After nine months, the 199 diapause larvae left appeared to differ in size according to the past treatment of the cultures. To find out whether the size of the resulting beetles would differ, they were weighed during the first day of adult life. In order to obtain the adults quickly, the diapause was broken by raising

TABLE IX.

The effect of new food on the weight (in mg.) of adults of *T. granarium* produced by diapause larvae.

Treatment	Females		Males	
	N	M ± S.E.	N	M ± S.E.
Crevice absent, new food ..	28	4·16 ± 0·22	34	1·43 ± 0·06
Crevice absent, stale food ..	39	3·23 ± 0·02	23	1·11 ± 0·03
Crevice present, new food ..	19	3·11 ± 0·09	12	1·16 ± 0·05
Crevice present, stale food ..	22	2·55 ± 0·08	22	0·96 ± 0·04

the temperature from 30 to 35°C. All the larvae became adult within the next 47 days. The weights given in Table IX show that the new food increased the size of the beetles of both sexes (significantly at the 0·001 level in all instances using an analysis of variance following Mather, 1949). The heaviest beetles were obtained with new food in the absence of a crevice and the lightest beetles occurred with stale food in the presence of a crevice, the remaining two combinations being intermediate. These results suggest that the larvae feed least in stale food in the presence of a crevice.

Behaviour of Normal Larvae.

To find whether normal larvae enter crevices, isolated larvae were bred from eggs, each in a tube with its own small crevice, on the mixture of wheat and wheatfeed. The crevices were examined once daily without disturbing the food.

TABLE X.

The behaviour of normal larvae of *T. granarium* bred in isolation.

	Little disturbance	Much disturbance
Number of larvae	22 larvae	40 larvae
Days in crevices per larva	1·8 days	3·8 days
Moults in crevices ..	1 moult	12 moults
Pupation in crevices ..	68%	90%

The results for the normal larvae are given in Table X. The longest period spent by a larva in a crevice was 10 consecutive days, but the periods were usually much shorter; some larvae moulted and many larvae pupated in the crevices. Forty larvae were severely disturbed every day by shaking the food. This disturbance approximately doubled the number of days on which normal larvae were found in the crevices (Table X).

In addition to the larvae included in Table X, three had a protracted larval period and presumably entered diapause, although they were found in the crevices for totals of only 0, 2 and 7 days, respectively. The proportion of diapause larvae bred in isolation is very low in comparison with the proportions obtained in cultures (25 and 54%, Table II).

Type of Larva hiding in the Fabric of Malt Stores.

In experimental populations the proportion of diapause larvae varied greatly and the diapause type of larva was the principal stage hiding in crevices. In order to discover which type predominated in crevices in maltings, samples of larvae were removed from their hiding places in the fabric of the stores and from standard crevices left on or near the malt.

All the larvae found were in their fourth or later instar, except possibly a very small number in the third instar. They were incubated at 30°C. in the laboratory. All normal larvae in the fourth instar should pupate at this temperature by the end of four weeks (Burges, 1957) so that all the remainder can be assumed to be diapause larvae. Some diapause larvae probably pupated during the first four weeks because, as will be shown in a later paper, an increase in temperature

causes many diapause larvae to pupate. Thus this technique often gives too small a number of diapause larvae.

The proportions of diapause larvae given in Table XI vary from 21 to 69 per cent.

TABLE XI.

The proportion of diapause larvae of *T. granarium* in samples collected from hiding places in malt stores.

Source	Total larvae	Diapause-type larvae (did not pupate) (%)	Normal and some diapause-type larvae (pupated) (%)
Hot-air chamber, crack in outer wall, ..	18	22	78
crack in floor	49	21	79
Bin, below bubble on kiln wall	13	69	31
Bin, walking on walls above malt 4 days old	29	45	55
Bin, below bubble on kiln wall	25	60	40
Standard crevice in loft above bin	40	45	55

Discussion.

The development and movements of larvae of *T. granarium* have been studied in the laboratory at 30°C., using a carefully controlled technique. The temperature is moderate in relation to the temperature range of the species, 21 to 40°C. (Hadaway, 1956). The behaviour pattern elucidated in these experiments can be related to observations made in maltings, ignoring for the present the effects of the large temperature changes that take place there.

A store full of infested malt can be likened to a large culture with resting places in all four walls, the top and the bottom. It appears that a proportion of the larvae in any infestation are normal, completing their development in a very short time, and the remainder delay pupation, entering diapause at some time after the third instar. Many of the latter wander. Some leave the food and rest in crevices in the fabric of the store; others accumulate in the spaces between the malt grains and the wall, usually resting on the wall just below the malt surface, and some enter empty malt grains. The larvae may remain in these places for a long time, occasionally leaving them to feed, presumably as the food stored in the fat-body is depleted. After feeding, some pupate and others re-enter diapause. Diapause larvae remaining in the malt would not be expected to pupate earlier than those in crevices, but they probably feed more and eventually produce heavier beetles. Since no inherent rhythmical pattern of behaviour of diapause larvae has been detected in the laboratory, it seems that the larval behaviour is regulated by the need to feed, by the availability of malt and by variations in temperature, which are often very irregular.

Survival through periods when no malt is available is accomplished by large numbers of the diapause larvae, which, hidden in the fabric of the store, are left behind at unloading. Due to their inactivity a large proportion of these diapause larvae escape the normal cleaning and spraying measures. These measures probably kill the small number of normal larvae using the crevices as moulting or pupation sites and also any hidden adults, all of which soon become active

again. At long and irregular intervals the hidden diapause larvae may feed on grain residues left behind after the store has been unloaded. After feeding, the larvae are most likely to resume diapause. Consequently this hidden population may survive for a number of years, although its strength is depleted very slowly by pupation and natural mortality. In laboratory experiments (page 413), 16 per cent. of diapause larvae had not pupated after four years.

Larvae in diapause may be activated by disturbance and by new food. When they are uncovered, as by the turning back of a folded sack, they slowly become active and search for other hiding places. The reaction of larvae to lesser degrees of disturbance in laboratory experiments was variable; sometimes a few larvae emerged from crevices to feed, this reaction probably being related to the state of the insects' food reserves. Larvae in crevices were able to detect new food given without disturbing them more than usual and some emerged, but after the initial burst the emergences decreased, even when the food was renewed regularly. As soon as the food becomes stale the larvae feed less, which must deplete their food reserves, and in this condition they are presumably readier to feed when stimulated by disturbance and new food. Both stimuli occur in malt stores. Larvae may be disturbed by vibration due to machinery and by movement of crevices in wooden structures caused by changing grain pressures. This disturbance by itself is not likely to be important in stimulating diapause larvae to emerge. On the other hand, new food loaded into the stores is probably a more powerful stimulant, particularly since it is often accompanied by some disturbance and especially when the diapause larvae have not fed for a long time. After feeding, some of the larvae will pupate and breed in the new malt, presumably producing offspring containing a proportion of normal larvae. When this new food is loaded into the stores, however, some larvae will not emerge and others, after feeding, will re-enter the crevices and resume diapause. Consequently, as observations in the maltings have shown, there is always a proportion of the population concealed in the fabric of the store, and the fabric cannot be disinfested completely by frequent loading and unloading of the store over a short period.

The normal insects produced in a bulk of malt breed rapidly, since their average developmental period in dry malt at 30°C. is 49 days (Hadaway, 1956). This rapid breeding is responsible for the main increase of the infestation in the bulk of malt. A proportion of the offspring produced in each generation will enter diapause and wander into the fabric of the store, thus completing the cycle.

The diapause of this species is facultative. Since some larvae can break their diapause when new food becomes available and the normal insects can breed rapidly without undergoing diapause, *T. granarium* is able to take advantage of a new favourable environment very rapidly.

In this discussion the very important effects of a changing temperature on diapause have not been considered and these will be described in later papers.

These observations probably apply equally well to food stores in the tropics, which differ from maltings mainly in the temperature and humidity conditions.

Summary.

The development of the khapra beetle, *Trogoderma granarium* Everts, and the cycle of movement of insects between the food and hiding places has been studied at 30°C. The results have been correlated with observations at maltings, its chief habitat in Britain.

In populations at 30°C., many larvae delay pupation and enter diapause, the remainder spending most of their time in the food and completing development quickly. The diapause larvae leave the food in the fourth and in later instars in search of hiding places. Disturbing the food stimulates the larvae to leave it a little earlier. Larvae resting in diapause moult occasionally, and at long and

irregular intervals they emerge, presumably to replenish their food reserves by feeding, after which some pupate and the rest hide again.

The hidden diapause larvae can persist for a very long time; in cultures, 16 per cent. remained after four years. Apparently, as the food stored in the fat-body is depleted, they become readier to emerge from the crevices to feed. Replacing stale food by new food causes some larvae to emerge and the effect of disturbing the larvae is variable. After feeding, some of these larvae complete development and the resulting adults breed, presumably producing both quick developing and diapause larvae among their offspring.

When denied a hiding place, the diapause larvae remain inactive in the food without increasing their rate of pupation. However, they feed more, producing heavier beetles, an effect also obtained by regularly providing fresh food.

It is concluded that when a malt store is loaded, some diapause larvae remain in the fabric of the store and others emerge and feed; after feeding, some larvae re-enter crevices and others complete development and breed; the offspring contain some diapause larvae, which accumulate in the crevices and on the walls just below the malt surface; after the malt is unloaded, diapause larvae may persist in empty stores for a number of years, because they can restore their food reserves by occasionally eating grain residues.

Acknowledgements.

I wish to thank Mr. T. E. Hughes of Birkbeck College, University of London, for advice and encouragement. A more detailed account of this work forms part of a thesis submitted for the degree of Ph.D. in 1956 and is held by the University of London. The work formed part of the research programme of the Pest Infestation Laboratory and this account is published with the permission of the Department of Scientific and Industrial Research.

References.

Burges, H. D. (1957). Studies on the Dermestid beetle *Trogoderma granarium* Everts. I. Identification and duration of the developmental stages.—*Ent. mon. Mag.* **93** pp. 105–110.

Hadaway, A. B. (1956). The biology of the Dermestid beetles, *Trogoderma granarium* Everts and *Trogoderma versicolor* (Creutz.).—*Bull. ent. Res.* **46** pp. 781–796.

Mather, K. (1949). Statistical analysis in biology.—3rd edn., 267 pp. London, Methuen.

Snedecor, G. W. (1938). Statistical methods applied to experiments in agriculture and biology.—388 pp. Ames, Iowa, Collegiate Press Inc.

BIOLOGICAL CONTROL OF INSECT PESTS IN BERMUDA.

By Fred D. Bennett

Commonwealth Institute of Biological Control

and

I. W. Hughes

Department of Agriculture, Bermuda.

Interest in the control of insects in Bermuda by means of the introduction of natural enemies dates back to 1875 when, according to Verrill (1902), the Surinam toad, *Bufo marinus*, was brought to the Colony from British Guiana by Captain Nathaniel Vesey in the hope that it would help to reduce the numbers of insects—particularly roaches—which were present on the Island. The toad is now extremely abundant and undoubtedly has some value as a predator of insects, slugs and snails. In general, biological control projects undertaken prior to 1945 were small and were carried out largely by officers of the local Department of Agriculture.

With the discovery of two scale insects, *Carulaspis minima* (Targ.) (previously recorded as *C. visci* (Schr.)) and *Lepidosaphes newsteadi* (Šulc), attacking the Bermuda cedar, *Juniperus bermudiana*, a marked increase in emphasis on biological control was brought about. In 1946 the Commonwealth Institute of Biological Control was asked to undertake a project to control these scales. This was followed by similar projects under the same direction against other agricultural and horticultural pests and during the past 14 years more than one hundred species of beneficial insects and other organisms have been introduced.

This paper lists the natural enemies which have been introduced since the liberation of the Surinam toad and attempts to assess the present position of those species which have become established. The projects are discussed separately below.

Biological Control Projects.

1. Cottony cushion scale, Icerya purchasi *Mask.*

The earliest record of *I. purchasi* in Bermuda is given by Bishop (1901). Ogilvie (1928) lists *Citrus*, roses, *Acalypha*, tamarisk and *Casuarina equisetifolia* as hosts in Bermuda. The Coccinellid, *Rodolia cardinalis* (Muls.), was introduced from the United States in 1902 by Bishop, who records its successful establishment. Ogilvie (1928) noted that effective control was achieved. However, it later became apparent that control was not entirely satisfactory. *Rodolia* is relatively inactive in the cooler months, and a significant increase in the scale population occurs during this period. The infestations are usually brought under control during the summer, when *Rodolia* breeds rapidly, but the host-plants suffer considerable damage before outbreaks are checked.

It was therefore decided to introduce the Dipterous parasite, *Cryptochetum iceryae* (Will.), from California, where it is effective in the coastal regions under conditions similar to those found in Bermuda. A small shipment was received in 1948 from which seven adults were liberated. In 1950, large shipments were obtained from California and adults were liberated throughout the Islands.

Investigations a few months later showed that this species was well established and effectively supplementing *Rodolia*. Five additional shipments were obtained in 1951 from which 15,000 parasites were liberated. In June 1956, no heavy infestations of *I. purchasi* could be found and in all instances when isolated scales were examined the majority were parasitised by *Cryptochetum*, even in areas where the Argentine ant, *Iridomyrmex humilis* (Mayr), accidentally introduced about 1948, was abundant.

2. Mediterranean fruit-fly, Ceratitis capitata (*Wied.*).

The Mediterranean fruit-fly was first recorded in the literature from Bermuda in 1890 by Riley & Howard, and it was the general belief that it had been present in Bermuda as early as 1865. Ogilvie (1928) records loquat, sapodilla, peach, pepper, *Citrus*, pawpaw, sugar-apple and guava as the main hosts in Bermuda. A concentrated effort to eradicate the Mediterranean fruit-fly was attempted in 1907. Inspectors were appointed to enforce the removal of all fruit from host-plants before they became susceptible to attack. The campaign was vigorously pursued for the next four years, but although the number of fruit-flies was considerably reduced, the pest was not eradicated and became as abundant as ever a few years later.

In 1905 a West Indian lizard, recorded as *Anolis* sp., was introduced from Jamaica as it was believed that this species was to a large extent responsible for the control of various fruit-flies in that island. The lizard, *Anolis grahami*, quickly became established, but it is difficult to say with any certainty whether or not the lizard has had any effect on local fruit-fly populations.

In 1926 and 1927 consignments of the Braconid parasite, *Opius humilis* Silv., were received from Hawaii. This insect was bred in the laboratory for a number of months and liberated in several localities. Russell (1936) recovered the parasite, but recent recovery attempts have failed, and it is now doubtful whether *O. humilis* is still present in the Colony.

3. Oleander scale, Pseudaulacaspis pentagona (*Targ.*).

First observed in Bermuda in 1917, infestations of *P. pentagona* were so heavy by 1920 that the oleander (*Nerium oleander*) was threatened with extinction. An extensive spraying programme giving temporary control in 1921 and 1922 cost the Government £4,000. In 1921, a small shipment of *Prospaltella berlesci* (How.) was obtained from the United States but no establishment occurred. From 1921 to 1924, several consignments of scale-infested twigs were received from Italy, and Ogilvie records the liberation of *Aphytis diaspidis* (How.), *P. berlesci* and *P. diaspidicola* (Silv.). In addition, the Coccinellids, *Chilocorus bipustulatus* (L.) and *Lindorus lophanthae* (Blaisd.), were received from Italy in 1924. Only *A. diaspidis* became established, and Ogilvie records this species to be completely controlling the scale. He states, however, that there is usually a slight increase in attack in the summer months. Since that time, *Aphytis* and to a lesser extent *Aspidiotiphagus citrinus* (Craw) and *A. lounsburyi* (Berl. & Paoli), both introduced accidentally—probably around 1940—, have kept *Pseudaulacaspis* fairly well under control. However, periodic outbreaks of oleander scale still occur. Damage from these outbreaks, while usually localised in nature, has nevertheless been a source of concern to the Bermuda Department of Agriculture.

In 1955, Dr. F. J. Simmonds, of the Commonwealth Institute of Biological Control, undertook an investigation to determine the causes of, and possible remedies for, the outbreaks of oleander scale. As a result of this investigation (Simmonds, 1958*a*), efforts were made to obtain additional parasites and predators to supplement the work being done by *Aphytis diaspidis*, *Aspidiotiphagus lounsburyi* and *A. citrinus*. From California, small numbers of *Aphytis proclia* (Wlk.), *A. lingnanensis* Comp., *Prospaltella perniciosi* Tower and *Comperiella bifasciata* How. were obtained for laboratory testing. They were not known to be parasites

of *Pseudaulacaspis*, but, inasmuch as they had been reared from related genera of scales, it was decided that they should be tried. Neither the laboratory tests nor subsequent small field liberations were successful. Approximately 500 examples of the Coniopterygid, *Spiloconis picticornis* Banks, were also shipped from California along with small numbers of *Aspidiotiphagus citrinus* and these were liberated in the field.

In addition, the following material was received from Trinidad during 1955–56: *Aphytis diaspidis* (Japanese and Trinidad strains), *Aspidiotiphagus citrinus*, the Coccinellids, *Cryptognatha simillima* Sic., *Coccidophilus citricola* Brèth., *Cryptognatha nodiceps* Mshl., *Cryptognatha* sp., *Pentilia insidiosa* Muls., *Prodilis* sp. nr. *gorhami* Brèth., *Chilocorus cacti* (L.), and the Nitidulid, *Cybocephalus* sp. Of these species, *Aphytis diaspidis*, *Aspidiotiphagus citrinus*, *Chilocorus cacti* and *Cybocephalus* sp. were already present in Bermuda as a result of earlier liberations. None of the remaining species became established.

During 1956 and 1957, over 100,000 adults of *Prospaltella berlesei* (strains from Japan and from the south of France) were released in Bermuda against *Pseudaulacaspis*. Despite the fact that this parasite was easily reared in the laboratory on oleander scale, no field recoveries were made (Simmonds, 1958*a*).

4. Palmetto scale, Comstockiella sabalis (*Comst.*).

This scale, which attacks *Sabal bermudiana*, the only endemic palm growing in Bermuda, was first recorded by Whetzel in 1921 (Ogilvie, 1928). At that time it was restricted to the eastern end of the Island, but by 1933 the scale had spread throughout the Colony. Details of parasite introductions are lacking, but brief mention is made in the annual reports of the Department of Agriculture of the importation of field-collected scale from Florida from which parasites were reared and liberated from 1926 to 1929. Mention of a parasite occurring locally was also made but no specific names were listed. However, in the annual report for 1933, Russell (1934) recorded *Aphytis fuscipennis* (How.), *A. mytilaspidis* (LeB.), *Encarsia portoricensis* How., and two undetermined species of Hymenoptera as parasites, and *Aleurodothrips fasciapennis* (Franklin) as a predator of the palmetto scale. In the annual report for 1934, Russell (1935) mentions *E. portoricensis* and *Physcus* sp. as occurring only in the eastern end of the Islands and described the transfer and establishment of these two species to several other areas. Waterston (1937) stated that the palmetto scale was successfully controlled by the introduction of *Physcus* sp. and *E. portoricensis*. No further mention of this scale is made in later reports and, although the scale occasionally causes yellowing of the fronds of palmettos, it is still under satisfactory control. Parasites and predators reared from the palmetto scale in 1956 were *Physcus* sp., *A. fasciapennis*, *Chilocorus cacti* and *L. lophanthae*. From this it would seem that *E. portoricensis* is no longer of importance as a control for this scale.

5. Coconut mealybug, Nipaecoccus nipae (*Mask.*).

This insect has been recorded as a serious pest on members of the family Annonaceae, guava, sapodilla, palms, avocado and several other plants in Bermuda. In 1926, an attempt was made to introduce the Encyrtid parasite, *Pseudaphycus utilis* Timb., from Hawaii, where it had successfully controlled the same mealybug. A few pieces of plant material possibly containing mealybugs parasitised by *P. utilis* were placed in the field, but no establishment occurred. In the same year, a few adults of the Coccinellids, *Cryptolaemus montrouzieri* Muls. and *Scymnus binaevatus* Muls., were received from California and liberated, but no establishment was recorded.

6. Onion thrips, Thrips tabaci *Lind.*

Waterston (1938) recorded *T. tabaci* as the major pest affecting the onion crop in Bermuda. In 1938, he arranged to obtain two consignments of the Eulophid

parasite, *Dasyscapus parvipennis* Gah., from Trinidad. Liberations took place in February and recoveries were made in March of the same year, but, inasmuch as no subsequent recoveries were made, it is concluded that the parasite did not become established.

7. *Potato tuber moth*, Gnorimoschema operculella (*Zell.*).

The potato tuber moth was first recorded from Bermuda in 1931. Heavy damage by this pest has been recorded in several instances, both in the field and in storage. Arrangements were made to obtain parasites from the Imperial Parasite Service (now the Commonwealth Institute of Biological Control) and in 1945 consignments of *Bracon gelechiae* Ashm. and *Chelonus phthorimaeae* Gah. were obtained from the California substation and liberated in several areas. *Arrenoclavus koehleri* (Blanch.) was introduced in 1946. In 1948, additional shipments of these three species as well as consignments of *Campoplex phthorimaeae* (Cushm.) were received from California. E. C. G. Bedford (*in litt.*) recovered *A. koehleri*, *B. gelechiae* and *Chelonus phthorimaeae* in 1948.

In 1951, only one of the introduced species, *B. gelechiae*, was reared from collections of potato tops (Bennett, 1952). The same species was again reared in June 1956. In addition to these introduced species, the following parasites have been recorded attacking potato tuber moth in Bermuda: *Apanteles dignus* Mues., *Agathis gibbosa* (Say), *Angitia compressa* (Cress.) and *A. blackburni* (Cam.).

Although one of the introduced species is well established, it is difficult to state whether it has reduced the infestations of tuber moth appreciably. In recent years the situation has become less critical due to improved cultural practices and better storage facilities. However, discarded tubers left in the fields and volunteer potato plants are often heavily attacked.

8. *Bermuda cedar scales*, Carulaspis minima (*Targ.*) *and* Lepidosaphes newsteadi (*Šulc*).

The endemic tree, *Juniperus bermudiana*, has been virtually exterminated during the past 12 years as a result of the ravages of two scale insects, *Lepidosaphes newsteadi* and *Carulaspis minima*.

L. newsteadi was first discovered in 1944, but it is probable that this scale was introduced prior to 1942. It spread rapidly between 1945 and 1947, killing many trees. *C. minima* is believed to have been introduced in 1942 but was not discovered until 1945, when infestations began to defoliate trees. The scale spread quickly throughout the Colony and by 1948 virtually every juniper was infested.

L. newsteadi was by far the more serious of the two scales during the early years of attack. However, in 1948, it became evident that *C. minima* was displacing *L. newsteadi* as the major killer of the juniper. By the end of 1948 it was difficult to find trees infested with *L. newsteadi*. The cause of this sudden decline in intensity of the infestation of this scale is unknown. Thompson (1954) suggests, but without conclusive evidence, that the decrease may have been due to its inability to compete with *C. minima*, which by 1948 had become island-wide in its distribution.

A vigorous programme of biological control, organised and directed by Thompson, was initiated in 1946 and continued until 1951. During this period, every effort was made to obtain and test parasites and predators of *L. newsteadi* and *C. minima* as well as of related species of scales. The project was abandoned only when the majority of the trees were dead or in such poor condition that they were unlikely to recover. The Commonwealth Institute of Biological Control undertook a mass breeding programme in California, shipping almost 700,000 scale-feeding beetles during the period 1948–1951. This was supplemented by a similar programme in Bermuda, which began with the completion of a new laboratory in 1949. When mass breeding was discontinued in 1951 more than 1,700,000 predacious beetles had been bred in the new laboratory.

In 1947, the first parasites and predators were introduced into Bermuda for release against the scales attacking the junipers. (The majority of the species which were introduced were intended for trial against *C. minima*, and unless *L. newsteadi* is mentioned as the host it can be assumed that all liberations were made against *C. minima*.) *Aphytis chrysomphali* (Merc.), a parasite of *L. ulmi* (L.) was secured from Ontario for trial against *L. newsteadi*. The predacious mite, *Hemisarcoptes malus* (Shimer), was also obtained from the same host in Canada and liberated in Bermuda against *L. newsteadi* and *C. minima*. *Lindorus lophanthae* and *Orcus chalybeus* (Boisd.) were obtained in March 1947 from California and released in Bermuda. In feeding trials both of these species appeared to be very promising. Several shipments of miscellaneous Coccinellids collected on bamboo, coconut and *Citrus* were shipped from Trinidad, B.W.I. *Azya trinitatis* Mshl., *A. luteipes* Muls., *Curinus coeruleus* (Muls.), *Chnoodes* sp. nr. *cinctipennis* Gorh., *Prodilis* sp., *Poria* sp., *Cryptognatha nodiceps*, *Scymnus* sp., *Pentilia* sp. and *Cybocephalus* sp. were among the species sent. An aphid feeder, *Cycloneda sanguinea* (L.), was also shipped and liberated against local species of aphids. *Zagloba ornata* (Horn), *Chilocorus distigma* (Klug), *Exochomus quadripustulatus* (L.), *Chilocorus stigma* Say (= *C. bivulnerus* Muls.), all Coccinellids, and the Encyrtid, *Habrolepis rouxi* Comp., were received from California. *Chilocorus nigritus* (F.) and *L. lophanthae* were obtained from Mauritius and liberated. From Italy two parasites of *Lepidosaphes ulmi*, *Anabrolepis zetterstedtii* (Westw.) and *Aphytis* sp., were received in addition to *C. bipustulatus*. In 1948, *C. bipustulatus* was obtained from France. *Eglus platycephalus* Muls. and *C. cacti* were received from Puerto Rico, while *Aphytis* sp. (origin China) was sent from California. In addition many of the species obtained in 1947 were again tried in 1948.

The mass rearing of Coccinellids and Nitidulids was started in California in 1948 and shipments of four Coccinellids, *Lindorus lophanthae*, *C. bipustulatus*, *Z. ornata* and *Cephaloscymnus occidentalis* Horn, and the Nitidulid, *Cybocephalus* sp. (origin China), were received.

In 1949, additional species, *Microweisia suturalis* (Schwarz), *Telsimia nitida* Chapin, *Lotis nigerrima* Csy., *L. neglecta* Muls. and *Pharoscymnus exiguus* Weise were received from California. Shipments of foliage heavily infested with *Lepidosaphes newsteadi* and *Leucaspis locwi* Colv. were obtained from Switzerland. From these scales the parasites, *Prospaltella aurantii* (How.), *Aphytis mytilaspidis* and *Azotus* sp., emerged and were liberated on infestations of *Lepidosaphes newsteadi*.

Mass breeding of predators was continued both in California and Bermuda in 1950. An additional species of *Cybocephalus* (origin South Africa) was received from California. *Exochomus quadripustulatus*, *Chilocorus bipustulatus*, *Scymnus* sp. and *Cybocephalus rufifrons* Rttr. were obtained from Portugal and tested on *Carulaspis minima*. *Chilocorus stigma* was received from Florida. The Neuropteron, *Semidalis aleyrodiformis* (Steph.) (Coniopterygidae), was found feeding on *Carulaspis* sp. in England and small numbers were sent to Bermuda for testing and liberation.

Further shipments of Coccinellids were received from Trinidad in 1951. *Azya trinitatis*, *A. luteipes*, *Curinus coeruleus*, *Lioscymnus diversipes* Champ., *Pentilia insidiosa*, *Cryptognatha nodiceps*, *P. confluens* (F.), *Chnoodes* sp., *Scymnus* sp., *Cryptognatha tumidiventris* Champ., *Zenoria revestita* Muls., *Prodilis* sp., *Pentilia castanea* Muls., *Exochomus bisbinotatus* Gorh. and at least three unidentified species were liberated from these shipments. Collections of Coccinellids were also obtained from Jamaica, the following species being present: *Chilocorus cacti*, *E. jamaicensis* Sic., *E. ritchici* Sic., *Procula douci* Muls., *Cycloneda sanguinea* (an aphid feeder) and *Scymnus* sp. (a mealybug feeder). *Chilocorus cacti* was mass reared in the laboratory. Stocks of *C. stigma*, *Microweisia misella* Lec.,

Cleis picta (Rand.), *Cycloneda sanguinea*, *Coccinella novemnotata* Hbst. and one undetermined species were obtained from Florida from juniper trees infested with *Carulaspis minima* and other scales.

The mass-rearing programme in California was terminated in 1951, shipments of *Lotis nigerrima*, *L. neglecta*, *Zagloba ornata*, *Pharoscymnus exiguus*, *Cephaloscymnus occidentalis*, *Lindorus lophanthae*, *Pentilia insidiosa* and *Cybocephalus* sp. (origin China) being sent during the final year. These shipments marked the close of the campaign to control the cedar scales in Bermuda. From these numerous introductions only a few species have become permanently established.

When *Carulaspis minima* was first discovered in Bermuda it was highly parasitised by *Aspidiotiphagus lounsburyi* and it was hoped that this parasite would bring the scale under control. This was not the case, even though parasitism as high as 90 per cent. was frequently recorded.

The Coccinellid, *L. lophanthae*, introduced from California and Mauritius in 1947, increased very rapidly in the field. In areas where this predator was particularly numerous practically all of the scale coverings were bitten and eaten. Despite this heavy scale mortality the trees continued to decline, and it was apparent that a relatively low infestation of scale, if sustained over a period of years, severely reduced the vigour and growth of the trees. Any marked build-up of the scale population caused partial or complete defoliation eventually resulting in the death of most trees.

Although several species of Coccinellids and Nitidulids introduced during 1947 and 1948 bred on *C. minima* in the laboratory and when confined in cloth sleeves in the field, very few of them survived for more than one or two generations when liberated. *Cybocephalus* sp. (Chinese origin) was recovered as late as 1952 but only in isolated instances. *Telsimia nitida* was present in the field a year or more after the final liberations but apparently has since died out. *Lotis nigerrima* behaved in a similar manner.

M. suturalis, introduced from California in 1949 and liberated in large numbers, became established and by 1950 was very abundant in the western parishes of Bermuda. In August 1950, from one branch about three ft. long, 46 adults, 110 larvae and three pupae were recovered. However, despite the abundance of *A. lounsburyi*, *Lindorus lophanthae* and *M. suturalis* at that time, the trees continued to decline and the project was abandoned. In June 1956, the only natural enemies found attacking *Carulaspis minima* were *L. lophanthae*, *M. suturalis*, *Hemisarcoptes malus*, *A. lounsburyi*, *Prospaltella* sp. and *Aphytis* sp.

While these parasites and predators were the only ones established on the cedar scale, a few additional species not adapted to breeding on this host have become established on other scales. *Chilocorus cacti* was bred in the laboratory from stocks obtained from Jamaica in 1951. It was liberated on several species of scales other than *Carulaspis minima* and became established on *Asterolecanium bambusae* (Boisd.), and has since been recorded on *Howardia biclavis* (Comst.), *Coccus hesperidum* L., *Coccus viridis* (Green), *Pseudaulacaspis pentagona*, *Saissetia nigra* (Nietn.), *Pulvinaria psidii* Mask., *Saissetia coffeae* (Wlk.) (*hemisphaerica* (Targ.)) and *Comstockiella sabalis*. *Cybocephalus* sp. shipped from Trinidad in 1947 and 1951 was recovered feeding on *Pseudaulacaspis pentagona* infesting oleander in 1955 and 1956.

As mentioned earlier, *Lepidosaphes newsteadi* ceased to be an important factor after 1948. Although light infestations examined in 1951 showed a high degree of attack by a Chytrid fungus, *Myiophagus ucrainica*, it seems improbable that this was the principal cause of the decline of this scale.

Severe hurricanes, one in October 1947 and three more in October and November 1948, resulted in wind and salt-spray damage causing severe burning and in many cases almost complete defoliation even to trees which were almost completely free from scales. Heavily infested trees suffered considerably more as

they were already in a somewhat weakened condition. When the surviving trees put out new foliage it was remarkably free from *L. newsteadi*. It is not intended to imply that the effects of the hurricanes brought the scale under control but that they masked any other factors contributing to the decline.

It is encouraging to note that a number of trees in the Island have survived the first heavy attack by *Carulaspis minima* and that although noticeably defoliated they have continued to live. Many of them are in as good a condition now as they were three years ago. Other trees exhibited a marked tolerance to the effects of *C. minima* and although infested for long periods were never seriously defoliated, often in striking contrast to neighbouring trees which died or suffered severely. It was also noteworthy that the occasional specimens of other species of juniper, *e.g.*, *J. virginiana*, *J. lucayana* and *J. silicicola*, were not defoliated to any extent, although moderate infestations developed. Thompson (1954) has suggested that the inability of *Juniperus bermudiana* to withstand a moderate infestation may be due to the isolation of Bermuda, whereas selection in the mainland species, *virginiana*, has through time produced tolerant strains. If this is correct, it seems probable, in view of the tolerance exhibited by a few of the trees, that were Bermuda an uninhabited island a scale-tolerant strain would reafforest the hillsides.

Plants grown from seeds of trees exhibiting tolerance have been planted in several areas. In addition a great many cedar seedlings are springing up in wastelands and on hillsides. Therefore it seems unlikely, as feared at one stage, that the Bermuda cedar will be completely annihilated. Whether the parasites and predators now established on *Carulaspis* have contributed to any extent is a matter of conjecture, although in the most recent survey Dustan (1959) found that parasitism was low and that there was little evidence of feeding by Coccinellids.

9. Canna leaf roller, Calpodes ethlius (*Cram.*).

The canna leaf roller was present in Bermuda as early as 1910. Due to the extensive damage caused by it, ornamental varieties of canna have not been planted on a large scale.

In 1953, several shipments of *Calpodes* eggs parasitised by *Trichogramma* sp. and *Ooencyrtus* sp. were received from Trinidad and the parasites liberated. A few adults of the larval parasite, *Elachertus meridionalis* Crwf., were also obtained from Trinidad. A survey in November 1953 indicated that both of the egg parasites were well established. Both species were recovered again in 1955. In June 1956, *Trichogramma* sp. was quite common whereas *Ooencyrtus* sp. was seen on only one occasion. Leaf-roller damage still occurs but is less serious than it was prior to the introductions of the parasites.

10. Harlequin bug, Murgantia histrionica (*Hahn*).

The harlequin bug was first observed a few years prior to 1949 but had not become sufficiently abundant until 1949 to cause severe damage to cabbages, mustard plants and related crops.

In 1953, small stocks of the egg parasite, *Ooencyrtus johnsoni* (How.), were obtained from Hawaii. Several thousand parasites were bred in the laboratory in Bermuda and liberated on infested plants. Recoveries were made a few months later. Egg-masses were collected in June 1956 but none was parasitised and it is concluded that permanent establishment was not achieved.

11. Long-tailed, citrus, and Mexican mealybugs, Pseudococcus adonidum (*L.*), Planococcus citri (*Risso*) *and* Phenacoccus gossypii (*Tns. & Ckll.*).

The first attempt to control mealybugs in Bermuda by biological means was made in 1926 when a small shipment containing 49 examples of *Cryptolaemus montrouzieri* was obtained from California and released against *Pseudococcus* spp. (see coconut mealybug, above). This effort was without success. In 1951,

arrangements were made to obtain parasites and predators from California for release against three of the most troublesome species, namely *Pseudococcus adonidum*, *Planococcus citri* and *Phenacoccus gossypii*.

The long-tailed mealybug, *Pseudococcus adonidum*, is commonly found attacking the sago palm (*Cycas revoluta*), oleander and *Pittosporum* The parasites, *Tetracnemus peregrinus* Comp., *Pseudaphycus angelicus* (How.), *Anagyrus fusciventris* (Gir.) and *Anarhopus sydneyensis* Timb., were all liberated against *Pseudococcus adonidum* during 1951. Additional shipments of *A. sydneyensis* and *Anagyrus fusciventris* were received during 1952 and 1953. Of these species, *Tetracnemus peregrinus* and *A. fusciventris* became permanently established, and most infestations of the long-tailed mealybug are now heavily attacked by one or both of these Encyrtids.

In 1955, *Cryptolaemus montrouzieri* was liberated on sage palm infested with *P. adonidum*. Permanent establishment was not achieved, however, despite the fact that small colonies survived for some months. The presence of the Argentine ant, *Iridomyrmex humilis*, and the tree lizard, *Anolis grahami*, appears to have been at least partly responsible for the failure of *Cryptolaemus* to become permanently established.

Other parasites and predators which were released against *P. adonidum* in 1955 were *Anagyrus pseudococci* (Gir.), the Hemerobiid, *Sympherobius barberi* (Banks), and the Coccinellids, *Hyperaspis jucunda* (Muls.), *H. lateralis* Muls. and *Scymnus sordidus* Horn. None of these species became established.

The citrus mealybug, *Planococcus citri*, has at times been a serious pest of croton (*Codiacum variegatum*) in Bermuda. Prior to 1951 the only parasite recorded as attacking this mealybug in Bermuda was the Encyrtid, *Leptomastix dactylopii* How. The Encyrtid, *Pauridia peregrina* Timb., was obtained from California in 1951 for release against this pest, and additional shipments of the same parasite were received during 1952 and 1953. Field recoveries of *P. peregrina* were made in 1953 and in 1956, indicating that the parasite is well established.

Small numbers of *L. dactylopii*, a species known to be already established (see above), were received from California in 1952 and released in areas where infestations of citrus mealybug were particularly heavy. This was done in the hope that the new stock of *Leptomastix*, possibly from a different race, would be more effective. Additional species of parasites and predators were introduced during 1953. These included *Leptomastidea abnormis* (Gir.), *Allotropa citri* Mues., *Pseudaphycus perdignus* Comp. & Zinna and *Cryptolaemus montrouzieri*. *Cryptolaemus* survived for several generations, but did not become permanently established on *Planococcus citri*. In 1955, the Coccinellids, *Scymnus sordidus*, *Hyperaspis jucunda* and *H. lateralis*, were tested against *P. citri* without success. The Hemerobiid, *Sympherobius barberi*, also failed on this host.

At the present time the citrus mealybug is not a pest of any importance on crotons. *L. abnormis* was recovered several times in May 1956 from *P. citri*, while *Pauridia peregrina* and *Leptomastix dactylopii* have also been recovered on a few occasions. These parasites have possibly been responsible for some measure of control, but other factors might very well be involved in the decline of this pest, or the decline may only be temporary.

Introductions of beneficial insects for the control of the Mexican mealybug, *Phenacoccus gossypii*, were restricted to the release, in 1951, of several shipments of the Encyrtid, *Accrophagus pallidus* Timb., which were obtained from California. This parasite was recovered in June 1956 in one area, but was heavily attacked by *Thysanus niger* (Ashm.) and its effectiveness was accordingly limited.

12. Soft scales.

There are more than a dozen species of scales in Bermuda which can be grouped under the broad heading of soft scales. The most economically important

of these are: *Coccus hesperidum*, *C. viridis*, *Pulvinaria psidii*, *Saissetia coffeae*, *S. nigra* and *S. oleae* (Bern.).

The first introduction of beneficial insects for the control of soft scales is recorded in 1949 when 255 examples of *Chilocorus angolensis* Crotch were received from California. This Coccinellid was originally obtained from South Africa where it is predacious on *Coccus hesperidum*. The beetles were liberated on soft scales attacking *Citrus*. Establishment was not achieved.

In 1953, outbreaks of green shield scale, *P. psidii*, became increasingly common, and it was decided at that time to initiate a programme of biological control. While the primary purpose of the introductions of the various parasites and predators of soft scales which were subsequently received was to achieve control of *P. psidii*, it was felt that the large number of suitable alternative hosts present in the Islands would greatly increase the chances of the introduced species becoming established. Many of the parasites which were received from California during the period 1953 to 1957 were known to attack *Coccus* and *Saissetia* spp., but were of unknown field value against *P. psidii*. However, laboratory tests indicated that the majority of these species could develop on green shield scale and liberations were therefore carried out.

Shipments of *Aphycus* (*Metaphycus*) *flavus* How., *A.* (*M.*) *luteolus* Timb. and *A.* (*M.*) *stanleyi* (Comp.) were received from California during 1953 and were liberated principally on oleanders infested with *P. psidii*. Some releases were also made on *Coccus* and *Saissetia* spp. attacking a variety of host-plants, including *Hibiscus* and *Citrus*. Additional shipments of the same three species were obtained in 1954. *A. flavus* was present in Bermuda prior to the liberation of the California shipments and is widespread. *A. stanleyi* is well established and was reared in large numbers from *Coccus hesperidum*, *S. oleae* and *S. nigra*, but only occasionally from *P. psidii* in May 1956. *A. luteolus* has not been recovered.

During the summer of 1953, two small shipments of *Microterys kotinskyi* (Full.) and *Aneristus ceroplastae* How. were obtained from Hawaii. Twelve adults of *M. kotinskyi* were liberated on a *Ficus* tree heavily infested with *P. psidii*, while 40 adults of *A. ceroplastae* were released on an oleander hedge infested with the same scale. *A. ceroplastae* has never been recovered, but *M. kotinskyi* was recorded as being quite common in 1954 in the general vicinity of the original liberation. Large numbers of *M. kotinskyi* were subsequently obtained from California during 1954 and 1955 and this species is now well established throughout the Islands.

The effectiveness of *M. kotinskyi* is somewhat curtailed by the fact that it often attacks scales which are almost fully matured, and in such cases parasitism does not prevent the scale from producing eggs (Simmonds, 1959). The presence of a secondary parasite, *Cheiloneurus pulvinariae* Doz., has also handicapped *Microterys*. However, during the past three years, parasitism by *Microterys* has been heavy in some areas and this species must be considered an important factor in the control of *P. psidii* at the present time. *Prochiloneurus* sp., which may be a tertiary parasite, was reared by Simmonds in 1955 but was not abundant enough to influence the situation.

Since 1954, continued efforts have been made to obtain additional parasites to supplement the work of *M. kotinskyi*. *Aphycus* (*Metaphycus*) *angustifrons* (Comp.) and *Coccophagus hawaiiensis* Timb. were both obtained from California in 1954 and 1955 but permanent establishment was not achieved. A small number of examples of a species of *Coccophagus* of the group of *C. lycimnia* (Wlk.) (= *lecanii* (Fitch)) was secured from São Tomé (Gulf of Guinea) in the spring of 1956. This species was reared through several generations on *P. psidii* in the laboratory, but field liberations were not successful. Additional parasites that were tried against this scale in 1956 and 1957 include *Coccophagus bogoriensis* (Kön.), *Aneristus* sp., both of which were received from Bangalore, India, as well as *Anicetus* sp.,

Aphycus (*Metaphycus*) sp. (origin India) and *Ancristus ceroplastae*, all from California. These introductions were without success. One further parasite, *Coccophagus mexicanus* Gir. was shipped from California for laboratory study in 1956 but was never liberated in the field.

The Coccinellids, *Cryptolaemus montrouzieri*, *Azya luteipes* and *Scymnus coccivora* Ram. Ayyar, were all liberated in considerable numbers against *Pulvinaria psidii* in 1956 and 1957. *Cryptolaemus* and *Azya* have achieved good control of this scale in several localised areas and are still maintaining themselves. However, as mentioned above, the effectiveness of these beetles appears to be severely limited by the tree lizards (Simmonds, 1958*b*) and it remains to be seen whether they can become permanently established. *S. coccivora* never became established.

Two species of Cecidomyiids obtained from Trinidad in 1956 were released against *P. psidii* but apparently these liberations were without success.

13. Red spider mite, Oligonychus ununguis (*Jacobi*).

Two small shipments of *Stethorus vagans* (Blkb.) and *S. picipes* Csy. were received from California in the summer of 1953 and were liberated against the mite, *Oligonychus ununguis*, which causes damage to the foliage of the endemic cedar, *Juniperus bermudiana*. Establishment was not achieved.

14. Tree lizards, Anolis *spp.*

Tree lizards are extremely abundant in Bermuda. The most common species is *Anolis grahami*, mentioned above. This is now distributed throughout the Island. A second species, *Anolis leachi*, was accidentally introduced, probably about 1945, and is now established in Warwick parish. Recently, what appears to be a third species of *Anolis* was found in the extreme western end of the Colony. This lizard has yet to be identified.

Investigations carried out by Simmonds (1958*b*) indicated that the tree lizards (*A. grahami* in particular) were preying heavily on beneficial insects, especially Coccinellids, that were being released against scale insects. In an effort to reduce the numbers of lizards, 200 examples of the kiskadee, *Pitangus sulphuratus*, a passerine bird of the family TYRANNIDAE, were introduced from Trinidad during the spring and summer of 1957. The birds have now passed through two winters and several pairs are known to have successfully reared young. It will be some time before any influence that the birds might have on the lizard population can be evaluated.

15. Snails.

There are more than 20 truly terrestrial snails in Bermuda, but only two species are presently of economic importance as agricultural pests. One of these is *Rumina decollata* (ACHATINIDAE), believed to have been introduced about 1876 by Governor Lefroy (Verrill, 1902). The other is *Otala lactea* (HELICIDAE), an edible snail brought into the Colony to be tried as a food in 1928, which subsequently escaped from captivity. It has become widely distributed and now poses a serious threat to certain vegetable and flower crops.

In January 1958, a shipment of predacious snails, *Euglandina rosea*, was sent from Hawaii to Trinidad where they were maintained at the Commonwealth Institute of Biological Control laboratory on local snails. Eggs were then shipped to Bermuda between January and April 1958. Laboratory tests carried out in Bermuda have indicated that *Euglandina* will attack both *O. lactea* and *R. decollata*. Field liberations have been made but no information is available on the result of these liberations.

Discussion.

It will be noted that the majority of species of beneficial insects introduced into Bermuda have failed to become established. This is not entirely unexpected

in view of the fact that several of the readily available entomophagous insects attacking species closely related to those of major importance in Bermuda were liberated without laboratory tests to determine whether they would develop on the Bermuda species. Additionally, many of the introduced species were obtained from areas differing considerably in climate and topography, and Bermuda conditions may not have been suitable. In other cases, the related species of host-insects from which the parasites and predators were obtained occupied quite different ecological habitats and, although breeding freely on the Bermuda pests in the laboratory, many of the beneficial species probably left the site of liberation in search for their accustomed microhabitat. For example, many of the Coccinellids obtained for trial against the cedar scales came from scales on botanically unrelated hosts and possibly were not adapted to an existence on cedar trees, despite the abundance of a host insect on which they bred readily in the laboratory. Although adequate laboratory and preliminary field studies might have suggested the unsuitability of many of the species it was not feasible to undertake them, due either to the urgency of the problem or to the lack of adequate personnel.

Establishment of parasites and predators has also been complicated by the presence of tree lizards and more recently by the accidental introduction of the Argentine ant, *Iridomyrmex humilis*. Tree lizards, *Anolis* spp., are extremely abundant on the Island, and studies carried out by Simmonds (1958*b*) indicate that they are capable of severely affecting the establishment of beneficial insects, particularly predacious beetles. It seems unlikely, however, that tree lizards were of any great importance during the campaign against cedar scales as they were rarely seen on cedar on unkept hillsides and were never beaten from the outer branches during recent surveys for Coccinellids. Nevertheless, a lizard was observed in 1951 feeding on adults of *Chilocorus cacti* a few minutes after they had been liberated on the main branches of a large juniper on a well-kept estate.

The Argentine ant was first recorded in Bermuda in 1948 and has since become numerous. It is now common in seven of the nine parishes of the Island, with small colonies present in the remaining two (Hughes, I. W. & Wingate, D. B., unpublished report, 1958). Simmonds (1958*a*) has already shown this ant to be influencing biological control in Bermuda, and judging from reports on investigations carried out in other areas in which the Argentine ant is found this influence can be expected to increase in importance (Flanders, 1943, 1951). Another ant, *Pheidole megacephala* (F.), now gradually being replaced by *Iridomyrmex humilis*, was seen carrying larvae of *Lindorus lophanthae* down the trunks of cedar trees. It was suggested (Bennett, 1951), as a result of preliminary experiments where ants were controlled, that *Pheidole* also was capable of causing a considerable reduction in Coccinellid populations.

It will be observed that some species of parasites and predators were introduced from more than one geographical area, and that on occasions species were liberated from foreign stocks despite the fact that they were already present in Bermuda. This was felt to be quite justifiable since forms that appear identical morphologically can often be separated by biological means and behave differently under varying conditions (Hafez & Doutt, 1954). Thus there was a possibility that stocks of a species of parasite from Japan would prove successful in Bermuda, even though stocks of the same species from France might have failed to become established.

Some of the parasites and predators which were introduced were collected incidentally to obtaining species of primary importance. For example, a number of Coccinellids obtained during cedar-scale investigations were known to be aphid feeders. Rather than discard this miscellaneous material, liberations were made against the specific host whenever possible.

In this paper no mention is made of the number of individuals of each species liberated, although whenever possible the general order of magnitude of liberations

has been given. Whereas thousands of adults of some species were released over a period of years, other species were received as single shipments and released in very small numbers. The fact that a species has been listed as introduced without success should not automatically preclude the usefulness of further liberations of that same species. For instance, *C. cacti* was established from liberations made in 1951 despite the failure of earlier liberations made in 1948.

Of the 15 biological control projects attempted in Bermuda, the most successful has certainly been the one directed against cottony cushion scale, *Icerya purchasi*. As a result of the work of *Rodolia cardinalis* and *Cryptochetum iceryae*, cottony cushion scale is no longer a pest of any importance in the Island. Several of the remaining projects appear to have resulted in very worthwhile results. Included in this group are those which have been conducted against oleander scale, *Pseudaulacaspis pentagona*, palmetto scale, *Comstockiella sabalis*, potato tuber moth, *Gnorimoschema operculella*, and mealybugs. Projects which are currently in progress and which cannot yet be evaluated include those dealing with the green shield scale, *Pulvinaria psidii*, tree lizards and snails.

Summary.

Projects undertaken on the biological control of insect pests in Bermuda since the first introduction of *Bufo marinus* in 1875 and including those still in progress are discussed. Work on 15 pests or groups of pests has been undertaken involving the introduction of over one hundred species of beneficial organisms.

Icerya purchasi Mask. is considered to be under excellent control as a result of the introduction of the Coccinellid, *Rodolia cardinalis* (Muls.), and the fly, *Cryptochetum iceryae* (Will.). *Pseudaulacaspis pentagona* (Targ.), a serious pest of oleanders, was brought under control about 1922 by the introduction of *Aphytis diaspidis* (How.). However, in recent years heavy infestations have periodically developed. In addition to *A. diaspidis*, the Aphelinids, *Aspidiotiphagus citrinus* (Craw) and *A. lounsburyi* (Berl. & Paoli), the Coccinellids, *Lindorus lophanthae* (Blaisd.) and *Chilocorus cacti* (L.), and the Nitidulid, *Cybocephalus* sp., now attack it.

Comstockiella sabalis (Comst.) at one time causing severe injury to the endemic palm, *Sabal bermudiana*, was brought under control by the introduction of *Physcus* sp. *Bracon gelechiae* Ashm. has been established on the potato tuber moth, *Gnorimoschema operculella* (Zell.), but satisfactory control has not resulted.

Two cedar scales, *Carulaspis minima* (Targ.) and *Lepidosaphes newsteadi* (Sulc), have decimated the stands of *Juniperus bermudiana* despite an extensive programme of biological control. *C. minima*, which proved to be the more serious, is attacked by the Aphelinids, *Prospaltella* sp., *Aspidiotiphagus lounsburyi*, *A. citrinus*, probably introduced with the scale, and the Coccinellids, *Lindorus lophanthae* and *Microweisia suturalis* (Schwarz), which were liberated in large numbers. The predacious mite, *Hemisarcoptes malus* (Shimer), and the fungus, *Myiophagus ucrainica*, were established on *Lepidosaphes newsteadi* which for unknown causes became very scarce.

Damage by *Calpodes ethlius* (Cram.), a pest of ornamental cannas, is less serious since the introduction of *Ooencyrtus* sp. and *Trichogramma* sp.

Several parasites were liberated to control various species of mealybugs. *Pseudococcus adonidum* (L.), serious on a number of ornamentals, is under satisfactory control as the result of the establishment of the Encyrtids, *Tetracnemus peregrinus* Comp. and *Anagyrus fusciventris* (Gir.). *Planococcus citri* (Risso) is now attacked by the introduced Encyrtids, *Leptomastidea abnormis* (Gir.) and *Pauridia peregrina* Timb., as well as by *Leptomastix dactylopii* How., which was present at the start of the investigation. *Acerophagus pallidus* Timb. has been recovered from the mealybug, *Phenacoccus gossypii* Tns. & Ckll.

The Encyrtid, *Microterys kotinskyi* (Full.), and the Coccinellids, *Azya luteipes*

Muls. and *Cryptolaemus montrouzieri* Muls., have been effectively established on the soft scale, *Pulvinaria psidii* Mask. Tree lizards, *Anolis* spp., which feed readily on *Azya* and *Cryptolaemus*, are considered undesirable and accordingly the passerine bird, *Pitangus sulphuratus*, has recently been liberated in an attempt to reduce their numbers.

Several species of parasites and predators were liberated against the soft scales, *Saissetia oleae* (Bern.), *S. coffeae* (Wlk.) and *Coccus hesperidum* L. *Aphycus stanleyi* (Comp.) is well established on *Saissetia* spp.

Although the Braconid, *Opius humilis* Silv., was established on the Mediterranean fruit-fly, *Ceratitis capitata* (Wied.), for a number of years it has now disappeared.

Parasites and predators introduced against *Nipaecoccus nipae* (Mask.), the onion thrips, *Thrips tabaci* Lind., and the red spider mite, *Oligonychus ununguis* (Jacobi), did not become established.

Projects at present in progress to control tree lizards, *Anolis* spp., and snails cannot yet be evaluated.

In the discussion a number of factors which may have contributed to the failure of establishment of some beneficial organisms are mentioned.

Acknowledgements.

The authors are indebted to F. J. Simmonds and R. G. Fennah for reading the manuscript and for suggestions made concerning the arrangement of material.

References.

Bennett, F. D. (1951). Report of the Acting Plant Pathologist for the year 1950.—*Rep. Dep. Agric. Bermuda 1950* pp. 19–29.

Bennett, F. D. (1952). Report of the Acting Plant Pathologist for the year 1951.—*Rep. Dep. Agric. Bermuda 1951* pp. 10–20.

Bishop, G. A. (1901). Report of the Board of Agriculture, Bermuda, 1901.—pp. 9–18.

Dustan, A. G. (1959). Report on a recent study of the cedar scale.—4 pp. Bermuda, Dep. Agric.

Flanders, S. E. (1943). The Argentine ant versus the parasites of the black scale.—*Calif. Citrogr.* **28** no. 5 pp. 117, 128, 137.

Flanders, S. E. (1951). The role of the ant in the biological control of homopterous insects.—*Canad. Ent.* **83** pp. 93–98.

Hafez, M. & Doutt, R. L. (1954). Biological evidence of sibling species in *Aphytis maculicornis* (Masi) (Hymenoptera, Aphelinidae).—*Canad. Ent.* **86** pp. 90–96.

Ogilvie, L. (1928). The insects of Bermuda.—*Bull. Dep. Agric. Bermuda* no. 15, 52 pp.

Riley, C. V. & Howard, L. O. (1890). A peach pest in Bermuda (*Ceratitis capitata* Wied.).—*Insect Life* **3** pp. 5–8.

Russell, T. A. (1934). Report of the Plant Pathologist, 1933.—*Rep. Dep. Agric. Bermuda 1933* pp. 28–36.

Russell, T. A. (1935). Report of the Plant Pathologist, 1934.—*Rep. Dep. Agric. Bermuda 1934* pp. 24–32.

Russell, T. A. (1936). Plant pathological report 1935.—*Rep. Dep. Agric Bermuda 1935* pp. 18–23.

SIMMONDS, F. J. (1958*a*). The oleander scale, *Pseudaulacaspis pentagona* (Targ.) (Homoptera, Coccidae) in Bermuda.—*Bull. Dep. Agric. Bermuda* no. 31, 44 pp.

SIMMONDS, F. J. (1958*b*). The effect of lizards on the biological control of scale insects in Bermuda.—*Bull. ent. Res.* **49** pp. 601–612.

SIMMONDS, F. J. (1959). The green shield scale, *Pulvinaria psidii* Mask. (Coccidae), in Bermuda.—*Bull. Dep. Agric. Bermuda* no. 32, 21 pp.

THOMPSON, W. R. (1954). Biological control work on cedar scales in Bermuda.—*Rep. 6th Commonw. ent. Conf. 1954* pp. 89–95.

VERRILL, A. E. (1902). The Bermuda Islands.—*Trans. Conn. Acad. Sci.* **11** pp. 413–956.

WATERSTON, J. M. (1937). Report of the Plant Pathologist, 1936.—*Rep. Dep. Agric. Bermuda 1936* pp. 22–27.

WATERSTON, J. M. (1938). Report of the Plant Pathologist, 1937.—*Rep. Dep. Agric. Bermuda 1937* pp. 24–37.

© Commonwealth Agricultural Bureaux, 1959.

OBSERVATIONS ON THE ASSOCIATION OF ANTS WITH COCCIDS OF TEA.

By G. M. Das, M.Sc., D.I.C., Ph.D.(Lond.)

Senior Entomologist, Tocklai Experimental Station, Cinnamara P.O., Assam.

(Plate X.)

More than 20 species of Coccids have been recorded as attacking tea in North-East India, but only a very few species cause appreciable damage in the plains of Assam and West Bengal. A number of species are, however, abundant at higher altitudes (in Darjeeling) and some of them are responsible for significant damage to tea, causing considerable die-back of the branches. In tea seed gardens in the plains, seed trees are seriously attacked by two or three species of Coccids.

Those species of Coccids that excrete honeydew and are consequently attended by ants are known to cause more damage to tea bushes and seed trees than the species which excrete no honeydew and are not therefore attended by ants.

In tea seed gardens, in which the tea trees may be as much as 20 ft. high, ant nests are common, and ants either harbour the honeydew-producing Coccids in their nests or attend them on exposed stems and leaves, while in tea bushes ant nests may be on the bushes or on shade trees in the vicinity. In the latter case, the ants may come down to attend Coccids infesting the tea bush.

Whatever damage the Coccids may cause to tea bushes, it is considered to be of lesser importance than the trouble caused by the ants, since the presence of the latter is a great nuisance to the people working in the field. Some of these ants bite so painfully that it becomes extremely unpleasant even to approach the inhabited bushes to pluck the tea and for other agricultural operations (Das, 1954). Instances are not uncommon where plucking had to be abandoned for some time in areas heavily infested with ants.

Ants utilise the honeydew excreted by the Coccids, in return for which they are said to protect them against their natural enemies (parasites and predators). Nixon (1951), however, in his review of the literature on the association of ants with aphids and Coccids, pointed out that the amount of protection afforded by ants through driving away parasites and predators has been much exaggerated.

In order to devise suitable measures for control of the ants nesting on tea bushes, some aspects of the relationship of these ants with certain common honeydew-excreting Coccids occurring on both tea bushes and tea seed trees in North-East India were studied. The results are presented in this paper.

Ants attending common Coccids of Tea in North-East India.

A list of ants associated with certain Coccids prevalent on tea bushes and tea seed trees is given in Table I. The list is, however, far from complete, since observations are being continued and some ants of lesser economic importance have yet to be determined.

Oecophylla smaragdina (F.).

This tree-nesting red ant is widely distributed in India. In tea plantations it occurs abundantly on shade trees and tea seed trees but it rarely forms its nests on tea bushes. It may, however, come down from shade trees to attend Coccids

occurring on tea bushes and, in seed gardens, *Coccus hesperidum* L. is usually found enclosed in its nest (Pl. X, figs. 1 & 2); it may also occur on stems and leaves outside the nests. *Coccus discrepans* (Green) is occasionally found on the thick stems of seed trees, attended by this ant. *Eriochiton theae* Green, however, occurs abundantly on seed trees in Assam and is invariably attended by *Occophylla*, but in the absence of the ant disappears completely. It attacks the stems and

TABLE I.

Coccids of tea, and the ants associated with them.

Coccids	Ants	Nests occurring on
(a) Enclosed in the nest of ant :		
Saissetia formicarii (Green)	*Crematogaster dohrni* Mayr	Tea bushes
	Crematogaster sp.	,, ,,
	Technomyrmex detorquens (Wlk.)	,, ,,
Coccus discrepans (Green)	*Crematogaster* sp.	,, ,,
Coccus hesperidum L.	*Oecophylla smaragdina* (F.)	Shade trees, tea seed trees and occasionally on tea bushes
Nipaecoccus vastator (Mask.)	*Polyrhachis affinis* Sm.	Tea bushes and shade trees
b) Attended by ants :		
Saissetia nigra (Nietn.)	*Pheidole sulcaticeps* Roger var. *punensis* Forel	In the ground
	Meranoplus sp.	,, ,, ,,
	Paratrechina sp.	,, ,, ,,
Eriochiton theae Green	*Oecophylla smaragdina*	Shade trees and tea seed trees
	Ceratopheidole bhavanae (Bingham)	In the ground
Saissetia coffeae (Wlk.)	*Technomyrmex modiglianii* Em. ssp. *elatior* Forel	In the ground
Coccus discrepans	*Oecophylla smaragdina*	Shade trees, tea seed trees, occasionally on tea bushes

lower surface of leaves but those occurring on the leaves are mostly the male nymphs. It is rarely found on tea bushes in the plains but is widely prevalent in Darjeeling, where it is considered to be one of the destructive pests, particularly of young tea. It is interesting to note that in this hill district *E. theae* is not attended by *Occophylla* but by *Ceratopheidole bhavanae* (Bingham) which has its nests in the ground.

The ant, *O. smaragdina*, is often found also to form small nests (Pl. X, fig. 3) on tea seed trees. These nests contain workers and larvae but no sexual forms. Dutt (1912) found such nests harbouring *Coccus hesperidum* on *Dalbergia sissoo*. When leaves infested by the Coccid are discovered on tea seed trees, the worker ants may construct " temporary nests " provided that the sites are suitable; otherwise, they attend the Coccids from their original nests. Under certain

circumstances, an old nest may be discarded and the entire colony may gradually move to the new nest.

Crematogaster dohrni Mayr.

The ant, *Crematogaster dohrni*, is very common on tea bushes and seed trees, and is considered to be the greatest nuisance of all ants forming nests on tea bushes. *Saissetia formicarii* (Green), which attacks the stems of the bushes, is invariably found enclosed in the nest of this ant (Pl. X, fig. 4) or of another species of *Crematogaster* (Pl. X, fig. 5). It has never been found on the exposed stems (outside the nests) and it appears that it can hardly exist unless imprisoned by the ants in their nests. In a commercial tea estate, control of *C. dohrni* led to the disappearance of the Coccid within three months; since then, no fresh nesting has occurred during the last five years. Conversely, where the Coccid was controlled the ant automatically disappeared. It was observed, in many cases, that breaking up of the nest and partial control of this ant was followed shortly by fresh nesting on the same site. Even complete destruction of ants on particular bushes or trees without controlling the Coccids led to the formation of fresh nests by ants coming from the adjacent bushes or trees.

Crematogaster sp.

A second species of *Crematogaster* has also occasionally been found to form nests on tea bushes and seed trees, harbouring *S. formicarii* in its nest. The relationship is similar to that existing in the case of *C. dohrni*.

Ceratopheidole bhavanae (Bingham).

C. bhavanae attends *Eriochiton theae* in Darjeeling and Terai, and has its nests in the ground. The ant colonies are few and the populations in them are not dense; the ants, therefore, can hardly be expected to remove more than a small portion of the honeydew excreted by the Coccid in a severe infestation. Obviously, most of the Coccid population dies out during the dry season as a result of honeydew accumulation and the subsequent growth of sooty moulds. Only a few examples of the Coccid, particularly young ones which excrete little or no honeydew, persist. On the other hand, under steady rains over a long period, when the honeydew is constantly washed off, the Coccid assumes serious proportions.

Polyrhachis affinis Sm.

P. affinis is a tree-nesting species, common on tea seed trees and shade trees but is also found on tea bushes. The mealybug, *Nipaecoccus vastator* (Mask.), may occasionally be found in small numbers in its nests (Pl. X, fig. 6).

Two further species, *Technomyrmex detorquens* (Wlk.) and *T. modiglianii* Em. ssp. *elatior* Forel, are occasionally found to form small nests of leaf-mould and other vegetable matter over colonies of *Saissetia formicarii*, which they attend.

Predators and Parasites.

The Coccids are usually kept under considerable check by their predators and parasites.

Predators.

Spalgis epius Westw.—The larva of this Lycaenid is rarely found among colonies of *E. theae* tended by *O. smaragdina*, but where the ants were prevented from attending the Coccid by grease banding (after removing all ants by hand), the Coccid colonies were completely destroyed by the predator within two weeks. This predator has never been found in colonies of *Coccus hesperidum* or *Saissetia formicarii*, whether tended by ants or not.

Microdon bellus Brun.—Only two larvae of this Syrphid were discovered and these were in a single nest of *Crematogaster dohrni* harbouring *S. fornicarii*. The larvae, which were apparently similar in shape to the Coccid, though larger in size when full-grown, were not attacked by the ant.

Coccinellids.—Coccinellid predators were not found amongst colonies of Coccids tended by ants. Both adults and larvae were, however, found to be active in ant-free colonies of *E. theae*, *Coccus hesperidum* and *C. discrepans*.

Parasites.

Insect parasites	Hosts
Encyrtidae, gen. et. sp. nov. ?	*Coccus hesperidum*
Coccophagus acanthosceles Wtstn.	*Saissetia formicarii*
Undetermined	*Eriochiton theae*

Sooty Moulds and Fungal Parasites.

Sooty moulds.

Honeydew excreted by Coccids forms an ideal medium for the growth of certain fungi, and a number of species of sooty moulds (*Capnodium* spp., *Phacosaccardinula theae* and *Meliola* spp.) were recorded as growing on it, the most common species being *Meliola* spp. (Tunstall & Sarmah, 1947). These fungi grow on the excretion falling on the surface of leaves, stems and vegetation underneath. Where the ants are in attendance, the fungi are, however, less in evidence.

When the predators were prevented from attacking ant-free colonies of *Coccus hesperidum* by enclosing the latter in muslin bags, the Coccids died out in two or three weeks, suffocated by the accumulation of honeydew and the subsequent growth of sooty mould covering them. A few Coccids, particularly young ones, scattered over the leaf margin, being isolated from the main colony, escaped destruction. Ant-free colonies of *E. theae* in muslin covers were similarly affected but not as rapidly as in the case of *C. hesperidum*.

In Darjeeling, where the population of *Ceratopheidole bhavanae* attending *E. theae* is small, and the ants are less efficient in removing the excretion, contamination with honeydew accumulation and subsequent growth of sooty moulds are primarily responsible for the disappearance of this Coccid during the dry weather, and the leaves and stems of the affected tea bushes are found to be completely covered with a dense black mass of sooty moulds. These sooty moulds, though not directly responsible for any damage to tea bushes, " interfere with the physiological processes of the plants " (Nixon, 1951).

Entomophagous fungi.

The spores of many entomophagous fungi that attack the Coccids are disseminated by the attending ants.

Aschersonia sp.—This fungal parasite attacks a number of species of Coccids occurring on tea. It appears to occur under warm, humid conditions and is occasionally responsible for reducing the Coccid populations to an extremely low level. The affected Coccid becomes a hard mass with yellowish-orange or pinkish-red cushions growing over it.

Septobasidium bogoriense.—This fungus, known as the " Velvet blight ", was at one time fairly common in Darjeeling but is now only occasionally to be found there. In the plains, it is rare. It attacks *E. theae* and several other species of Coccids in Darjeeling and, after destroying the colonies, spreads over the stems of the tea, occasionally to the lower surface of the leaves (Tunstall & Sarmah, 1947). Several other species of *Septobasidium* (*e.g.*, *S. pilosum*, *S. tuberculatum* and *S. theae*) are also known to attack Coccids.

Relative Populations of the Coccids and attendant Ants.

Way (1954*a*, 1954*b*) came to the conclusion that the major part of the food supply of the ant, *Occophylla longinoda* (Latr.), is met from the honeydew excreted by the Coccid, *Saissetia zanzibarensis* Williams. In this connection, population studies of the ant *Crematogaster dohrni* in the nests formed on tea bushes, in an estate near Tocklai, and of *Saissetia formicarii* imprisoned therein were made, the results of which are given in Table II.

TABLE II.

Relative populations of *C. dohrni* and *S. formicarii*.

Nest	Number of adult ants in nest*	Number of Coccids		Total
		Adults	Nymphs*	
1. Sexual forms present	28,068	111	923	1,034
2. „ „ „	53,000	15	80	95
3. „ „ „	30,900	120	1,025	1,145
4. Sexual forms absent	2,054	116	512	628

* The figures are only approximate, as the ants that were outside were not included, and as the young nymphs of the Coccid are difficult to count correctly.

It would appear from the above table that the populations of the ant (larvae not included) in the nests that contain sexual forms are extremely high, in comparison with the Coccid populations therein. Considering the large population of the ant, it is doubtful if a major part of the food requirement of the ant can be met from the honeydew excreted by such a small colony of the Coccid, the majority of which are young nymphs excreting little or no honeydew. In the three nests with queens, the proportion of ants to Coccids was 49 to 1; it is difficult to see how one Coccid could support such a large number of ants with its honeydew excretion.

When the stems inside a big nest are badly damaged by persistent attack, and the Coccid populations are reduced to a low level, new nests are constructed and the ants remove the Coccids to more suitable sites. Most of the new nests are small and contain no sexual forms of the ant, but if the Coccid population builds up, the nest is progressively enlarged. When an old nest has to be abandoned, the sexual forms and larvae are gradually transferred to the new and bigger secondary nest, and ultimately the whole colony moves into it. The workers from smaller nests are found constantly visiting the primary nest which contains sexual forms and it may be that they contribute some honeydew, derived from the smaller nests, to the maintenance of the brood in the primary nest, but this amount is not likely to be very high.

The population of *Coccus hesperidum* enclosed in the nest of *O. smaragdina* is extremely low in comparison with that of the ant. Although workers also attend *E. theae* and *C. hesperidum* occurring on the stems outside the nests, the populations of these Coccids are not considered to be sufficiently high to be able to support with honeydew more than a very small proportion of the ant population of a big nest.

It appears, therefore, that a considerable part of the food for the ant population

in a nest must come from other sources, and the insects attacking or visiting tea bushes and seed trees and even those found on the soil surface are considered to form the major part of their requirements.

It was formerly thought by a considerable number of planters that the presence of the ant, *Crematogaster dohrni*, on tea bushes was the means of protecting an estate from other insect pests. Though this was refuted by Watt & Mann (1903), and later altogether rejected by planters, there is enough evidence to show that the ant, *O. smaragdina*, considerably reduces insect pests on seed trees. The fact that the ants themselves are a great nuisance to people working in fields, and that they foster the Coccids, outweighs the benefit derived from any check they may exercise on other pests of tea.

On seed trees inhabited by *O. smaragdina*, insect pests are rare, with the notable exception of Psychid caterpillars, which are protected in larval cases, and Coccids, which thrive in association with the ant. How far the ant is responsible in destroying the population of the tea seed bug, *Poecilocoris latus* Dall., has not yet been assessed, but there is some indication that the Pentatomid is less prevalent on trees inhabited by the ant.

A large number of worker ants are found to roam about from branch to branch, often crossing to adjacent trees and occasionally coming down to soil surface to forage, and they fiercely attack any insects they come across. Pollinating insects are not spared. In addition to insects, the ants have been found to attack centipedes, millipedes, spiders, earthworms, etc., and drag them into their nests. On one occasion, the ants attacked an atlas moth, which was overpowered and carried away. With a wide range of food available on seed trees and on the ground underneath, the dependence of this ant on the Coccids for food appears to be small. Nevertheless, the Coccids provide the ant with an easily accessible rich food (Nixon, 1951), and at certain times, when other insects are rare, this, being the only dependable food available to them, is probably the main attraction.

Use of Ants to control the Tea Seed Bug.

Attempts to control insect pests of plants by using predaceous ants have not always proved to be satisfactory, since the Homopterous insects fostered by the ants become serious pests. Nixon (1951) suggested that ants to be used in combating insect pests should have a loose relationship with the Coccids with which they are associated. *Oecophylla* is, however, of considerable importance, being predominantly predaceous and more aggressive than are any other ants in the tea gardens. *O. smaragdina* has proved satisfactory in protecting plants from some insects pests. It controls the Pentatomids, *Tessaratoma papillosa* (Dru.) (Groff & Howard, 1925) and *Rhynchocoris serratus* (Don.) (Garcia, 1935), on *Citrus*, and the Coreid, *Amblypelta cocophaga* China on coconut (Phillips, 1940; O'Connor, 1950). *O. longinoda* was found to be of great value in controlling certain coconut pests, particularly *Pseudotheraptus wayi* Brown, another Coreid, which damages developing coconut fruits in East Africa. The damage caused by the Coccids associated with the ant is considered to be insignificant in comparison with the benefit derived from protection against *P. wayi* (Way, 1954*a*).

On the other hand, Froggatt (1937) doubted the usefulness of *O. smaragdina* in controlling a Hispid beetle, *Promecotheca*, on coconuts in New Guinea since it might interfere with pollination, in addition to transporting and protecting scale insects. When the ant was introduced into a coffee plantation to control caterpillars of the Sphingid, *Cephonodes hylas* (L.), it became established only on those bushes where Coccids were present; the colonised bushes however, became less healthy as a result of the damage by Coccids fostered by the ant (Corbett, 1937).

The possibility of using *O. smaragdina* for controlling *Poecilocoris latus* in seed gardens may be considered when other aspects of its use, *e.g.*, how far it will

affect cross-pollination by destroying pollinating insects, and the increased amount of damage by Coccids fostered by it, are critically examined.

The Protection afforded by Ants to Coccids from their Natural Enemies.

The degree of parasitism is low in the Coccid colonies enclosed in the ant nests, usually not exceeding 6 per cent. of the population but, where the Coccids are exposed, parasitism is much higher. Information on parasitism in three species of Coccids associated with ants and collected on Tocklai and neighbouring estates is given in Table III.

TABLE III.

Percentage parasitism of Coccids associated with ants.

	No. scales	No. parasitised	Percentage parasitised
Saissetia formicarii enclosed in the nest of *Crematogaster dohrni* :			
Nest 1	1,034	25	2·42
„ 2	628	9	1·43
„ 3	96	9	9·47
„ 4	1,145	62	5·41
Coccus hesperidum enclosed in the nest of *Oecophylla smaragdina* :			
Nest 1	1,078	62	5·75
„ 2	279	14	5·02
„ 3	8,732	523	5·99
Eriochiton theae attended by *O. smaragdina* on exposed stems :			
Nest 1	229	45	19·65
„ 2	290	51	17·58

The red ant, *O. smaragdina*, attending *E. theae* was under observation for some time in the field. The adult parasites are often seen to move aside to avoid approaching ants, but the worker ants do not seem to take any particular notice of them. Although there is no direct interference from the ants, the disturbance caused to the parasites, in their search for suitable Coccids in which to oviposit, by the constant movements of the ants soliciting for honeydew, appears to reduce the rate of parasitism though not appreciably.

Workers of *O. smaragdina* are so aggressive that any foreign bodies are fiercely attacked, whether they constitute their food or not; but the adult Hymenopterous parasites are so small that when they are moving slowly at least they hardly arouse any suspicion in the ants and thus escape destruction. In the absence of attendant ants, the parasitism appears to be slightly increased, but no accurate estimation was possible as the Coccids were subsequently destroyed by predators. Herzig (1937) states that " ants react to the swift moving bodies behaving as though an attack is directed against themselves, and accidentally protect Aphids ". Nixon (1951) came to the conclusion that aphids and Coccids are not protected because they constitute a valuable source of food, but there is enough evidence to show that they are benefited by the accidental protection.

In the presence of the attendant ant, *O. smaragdina*, the larva of the Lycaenid, *Spalgis epius*, is rare in the colonies of *E. theae* on tea seed trees (in Upper Assam). But where the ants were prevented from tending them, the predator

appeared within a week's time and destroyed the Coccids. Of the other predators, both adults and larvae of Coccinellids were also found but larvae of lacewings (*Chrysopa* spp.) were fewer.

When the larvae of *Spalgis epius*, collected from ant-free colonies, were introduced into the colonies of *E. theae* tended by *O. smaragdina*, they destroyed the Coccids without being molested by the ants, but when the naked larvae of Coccinellid beetles were introduced they were immediately killed. The larvae of the Lycaenid cover themselves with woolly fluff and the remains of the Coccids they have eaten, and thus protect themselves from their enemies. When introduced after removing their protective covering, they were immediately seized and destroyed. Glover (1930) observed that *Eublemma amabilis* Moore, a predator of the lac insect, *Laccifer lacca* (Kerr), is attacked by the ants, *Camponotus compressus* (F.) and *Solenopsis geminata* ssp. *rufa* (Jerd.). Kirkpatrick (1927) found that when a new predator was introduced into a colony of the mealybug, *Planococcus* (formerly *Pseudococcus*) *kenyae* (Le Pelley), on coffee attended by the ant, *Pheidole punctulata* Mayr, the latter could easily recognise it and attacked it violently. Krishna Ayyar (1935) also observed that *Camponotus compressus* fostering aphids and Coccids attacked Coccinellid beetles but not their larvae, which had a spiny body.

It appears that the ant, *O. smaragdina*, cannot distinguish the larva of the Lycaenid from the Coccid, *E. theae*, because of its protective covering, but a naked Lycaenid larva is as easily recognised and attacked as any other insect that happens to be near the nest.

The absence of larvae of the Lycaenid, or any other predaceous larvae having a protective covering over their body, from the colonies of *E. theae* tended by the ant, *O. smaragdina*, appears to be due to the fact that the ants prevent the adults from ovipositing either by killing them or driving them away. If, by any chance, the eggs are laid in or near the colonies of the Coccid, or the larvae by some means gain access to the colonies, they continue to prey upon the Coccids without being molested by the attending ants. The same may be true with the larvae of *Chrysopa* or Coccinellids having similar protective covering. Guenther (1925) and Kirkpatrick (1927) record that the larvae of Chrysopids protect themselves from the attention of ants by covering their body with a waxy covering and the remains of Coccids, and only those that appear to have moulted recently and have no protective covering are attacked. On the other hand, Herzig (1937) states that the slow-moving larvae and adults of Coccinellid beetles are seldom interfered with by the attendant ants while they are feeding.

The larva of *Microdon bellus* resembles *Saissetia formicarii* in general appearance though when full-grown it is larger. The presence of these larvae in the colony, unmolested by *Crematogaster dohrni*, appears to be due again to the fact that the ant cannot differentiate between predator and Coccid. The larva of *Microdon* sp. that occurs in the colonies of the tea aphid, *Toxoptera aurantii* (Boy.), is even palpated for honeydew by the attending ant, *Crematogaster* sp., which, however, being unsuccessful passes on. It is, therefore, assumed that the ants take the larvae of *Microdon* spp. to be Coccids, a source of food, whether they occur in the colonies of Coccids or aphids. Nixon (1951) came to the conclusion that " predators apparently achieve immunity from ant molestation by resembling their prey ".

Migration of the Coccids, *Coccus hesperidum* and *E. theae*, usually takes place during the early nymphal stage, though occasionally nymphs may be aided by *O. smaragdina* in their dispersal, but the nymphs of *S. formicarii* are prevented from escaping from the nests of *Crematogaster dohrni* and *Crematogaster* sp. by the ants, which imprison them unless occasions arise which necessitate their removal to other suitable sites, in which case the ants themselves transport them.

O. smaragdina does not appear to transport *Coccus hesperidum* and *E. theae* from the healthy leaves and stems under normal conditions, but on several occasions it has been found to carry specimens of *C. hesperidum* from the withered leaves and die-back stems into the nests. Dutt (1912) also found that this ant removed *C. hesperidum* from withered leaves of *Dalbergia sissoo* to fresh ones.

Under experimental conditions the ants also carried living examples of *C. hesperidum* from the withered tea leaves in broken nests into their new nests, but only young individuals were to be found inside a few days later. In order to find out the fate of the sedentary Coccids that are carried into the nests, a known number of adult females of *C. discrepans* were placed by means of a scalpel near two small nests which were known to contain *C. hesperidum*; they were immediately seized by the ants and carried into the nests. One of the nests was examined after six hours and the other after 24 hours, but not a single specimen of *C. discrepans* could be found either inside or near either nest and it is logical to suppose that they had been eaten by the ants. Similarly, when the sedentary females of *C. hesperidum* were being dislodged from the stems with a scalpel, the attending ants immediately seized them and carried them into their nests, and their fate was probably the same as that of the adult females of *C. discrepans*.

A small nest of *O. smaragdina* containing *C. hesperidum* was placed at the lower part of an isolated tree which was free from any Coccid infestation. The ants transferred the individuals of *C. hesperidum* from the withered leaves of the nest into a new nest formed at the top of the tree. The nest was opened for examination after 12 days and only young Coccids were found established therein. The sedentary forms which had also been carried into the nest could not be traced. *O. smaragdina* was never found to eat the nymphs and adults of *C. hesperidum* from healthy shoots. Negi, Misra & Gupta (1930), Glover (1930) and Strickland (1947), however, found ants destroying larvae of the Coccids associated with them. Nixon (1951) considers that the ants may eat active forms of Coccids but not those which have become sedentary and are excreting honeydew. Smith & Armitage (1931) found ants to be more aggressive when the Coccids are relatively few in numbers. Way (1954*b*) observed *O. longinoda* killing both sedentary adults and active nymphs of *Saissetia zanzibarensis* when the latter produced honeydew in excess of the food requirement of the ant colony.

As stated above, *S. formicarii* is always housed by the ants, *Crematogaster dohrni* and *Crematogaster* sp., in their nests. In no case could the Coccid be found outside on the exposed stems or leaves of a large number of tea bushes and seed trees that were thoroughly examined. In rare instances, young nymphs may escape from the nest and settle down somewhere on the stems, to be subsequently enclosed in small nests formed by the ants. The ants, which imprison them in their nests, are primarily responsible for dissemination of the Coccid when it becomes necessary to remove them to more favourable sites for feeding. This usually occurs when the infested branches inside the nests are badly damaged or dying back as a result of persistent attack by Coccids, or due to some other reason. The ants then construct new nests on healthy branches of the same or adjacent bushes or trees, and transfer the Coccids to them. For example, small nests can be found in numbers after the pruning of tea bushes. This was confirmed experimentally by detaching infested branches below the nests, and leaving them on the ground nearby; the ants constructed several small nests on healthy stems, and transferred the Coccids to them, but only young individuals were subsequently found to have established themselves. Dutt (1912), Hough (1922), Edwards (1935), Betrem (1936), Strickland (1947), Way (1954*b*) and others have recorded dissemination of Coccids by ants, and it was even believed in the early days of tea plantation that *O. smaragdina* actually transported Coccids from place to place to found fresh colonies of them in convenient situations (Watt & Mann, 1903).

Summary.

Certain species of Coccidae that excrete honeydew and are attended by ants or enclosed in their nests are quite prevalent on tea bushes and seed trees in the plains of Assam and West Bengal but those which are not attended by ants are kept under considerable check by the activities of their natural enemies. In Darjeeling, where the natural enemies are fewer, a number of species occur abundantly and are often responsible for serious damage to tea.

From the studies of the relative population of the ant, *Crematogaster dohrni* Mayr and the Coccid, *Saissetia formicarii* (Green), occurring on tea bushes it is doubtful if more than a small portion of the food requirement of the vast ant population in the nests which contain sexual forms could be met from the honeydew excreted by the small number of Coccids enclosed therein. The major part of food must, therefore, come from other sources. Insects attacking or visiting the tea bushes and tea seed trees or even those found on the ground appear to constitute the major part of the food of the ants, *C. dohrni* and *Oecophylla smaragdina* (F.).

Several factors are responsible for the decrease in the population or disappearance of the Coccids in the absence of attendant ants. In the plains, *Eriochiton theae* Green, *Coccus hesperidum* L. and *S. formicarii* entirely disappear in the absence of attendant ants either due to the activities of their natural enemies or by contamination with honeydew accumulation or both. Parasitism may be slightly higher in ant-free colonies, but no estimation was possible since, in the absence of ants, the Coccids are quickly destroyed by predators.

The ants do not protect the Coccids from Hymenopterous parasites; but their active movements hinder the parasites in their efforts to oviposit, and this leads to a reduction in the rate of parasitisation.

In the presence of the ants, *O. smaragdina* and *Crematogaster dohrni*, predators are rare; they are destroyed as are any other insects or any foreign bodies that happen to be near their nests, whether they constitute food or not. The larvae of predators which have a protective covering or which resemble Coccids, if they happen to have gained access to the Coccid colonies, are not attacked by the ants, because they are not recognised as different from the Coccids.

O. smaragdina does not normally transport Coccids, though young nymphs of *E. theae* and *Coccus hesperidum* may be aided in their dispersal, but *Crematogaster dohrni* and *Crematogaster* sp. are primarily responsible for the dispersal of *S. formicarii* and this takes place when an occasion arises to remove the Coccid to more favourable sites.

O. smaragdina does not destroy the nymphs and sedentary form of *Coccus hesperidum* for food, but sedentary forms which are unable to establish themselves on transfer from withered leaves to a new nest are eaten.

With the control of the attendant ants, the honeydew-producing Coccids disappear or at least they become rare. Conversely, where the Coccids are controlled, the ants automatically disappear.

Acknowledgements.

The writer is indebted to Mr. H. Ferguson, Director, Tocklai Experimental Station, for his comments and for permission to publish this paper; to the Director of the Commonwealth Institute of Entomology for the identification of the ants and a number of the Coccid specimens; and to Mr. Nixon for his suggestions on certain points during discussion.

References.

Betrem, J. G. (1936). Gegevens omtrent de biologie van de dompolanluis (*Pseudococcus citri*) en de lamtoroluis (*Ferrisiana virgata*).—*Arch. Koffiecult. Ned.-Ind.* **10** pp. 43–84. (*Rev. appl. Ent.* (A) **26** p. 606.)

Corbett, G. H. (1937). Division of Entomology. Annual report for the year 1936.—*Gen. Ser. Dep. Agric. S.S. & F.M.S.* no. 26 pp. 29–48.

Das, G. M. (1954). Ant nests on tea bushes.—*Two and a Bud* **1** no. 2 pp. 16–18.

Dutt, G. R. (1912). Life histories of Indian insects. IV (Hymenoptera).—*Mem. Dep. Agric. India* Ent. Ser. no. 4 pp. 183–267.

Edwards, W. H. (1935). Report of the Government Entomologist.—*Rep. Dep. Agric. Jamaica 1934* pp. 24–28.

Froggatt, J. L. (1937). *Promccotheca antiqua* Wse. Leaf pest of coco-nuts.—*New Guinea agric. Gaz.* **3** no. 2 pp. 21–22.

Garcia, C. E. (1935). A field study on the citrus green bug *Rhynchocoris serratus* Donovan.—*Philipp. J. Agric.* **6** pp. 311–325.

Glover, P. M. (1930). Entomological aspects of lac research in India.—*Bull. ent. Res.* **21** pp. 261–266.

Groff, G. W. & Howard, C. W. (1925). The cultured citrus ant of south China.—*Lingnaam agric. Rev.* **2** pp. 108–114.

Guenther, K. (1925). Untersuchungen an landwirtschaftlich schädlichen Insekten in Brasilien.—*Z. angew. Ent.* **11** pp. 400–414. (*R.A.E.* (A) **14** p. 130.)

Herzig, J. (1937). Ameisen und Blattläuse. (Ein Beitrag zur Ökologie aphidophiler Ameisen.)—*Z. angew. Ent.* **24** pp. 367–435. (*R.A.E.* (A) **26** p. 195.)

Hough, W. S. (1922). Observations on two mealy bugs, *Trionymus trifolii*, Forbes, and *Pseudococcus maritimus*, Ehrh. (Hom., Coccidae).—*Ent. News* **33** pp. 171–176.

Kirkpatrick, T. W. (1927). The common coffee mealy-bug (*Pseudococcus lilacinus* Ckll.) in Kenya Colony.—*Bull. Dep. Agric. Kenya* no. 18, 110 pp.

Krishna Ayyar, P. N. (1935). The biology and economic status of the common black ant of South India, *Camponotus* (*Tanaemyrmex*) *compressus* Latr.—*Bull. ent. Res.* **26** pp. 575–585.

Negi, P. S., Misra, M. P. & Gupta, S. N. (1930). Ants and the lac insect (*Laccifer lacca*).—*J. Bombay nat. Hist. Soc.* **34** pp. 182–188.

Nixon, G. E. J. (1951). The association of ants with aphids and Coccids.—36 pp. London, Commonw. Inst. Ent.

O'Connor, B. A. (1950). Premature nutfall of coconuts in the British Solomon Islands Protectorate.—*Agric. J. Fiji* **21** pp. 21–42.

Phillips, J. S. (1940). Immature nutfall of coconuts in the Solomon Islands.—*Bull. ent. Res.* **31** pp. 295–316.

Smith, H. S. & Armitage, H. M. (1931). The biological control of mealybugs attacking citrus.—*Bull. Calif. agric. Exp. Sta.* no. 509, 74 pp.

Strickland, A. H. (1947). Coccids attacking cacao (*Theobroma cacao*, L.), in West Africa, with descriptions of five new species.—*Bull. ent. Res.* **38** pp. 497–523.

Tunstall, A. C. & Sarmah, K. C. (1947). Notes on stem diseases of tea.—*Memor. Tocklai exp. Sta. Indian Tea Ass.* no. 16, 77 pp.

Watt, Sir G. & Mann, H. H. (1903). The pests and blights of the tea plant.—2nd edn., 429 pp. Calcutta.

Way, M. J. (1954*a*). Studies of the life history and ecology of the ant *Oecophylla longinoda* (Latreille).—*Bull. ent. Res.* **45** pp. 93–112.

WAY, M. J. (1954*b*). Studies on the association of the ant *Oecophylla longinoda* (Latr.) (Formicidae) with the scale insect *Saissetia zanzibarensis* Williams (Coccidae).—*Bull. ent. Res.* **45** pp. 113–134.

© Commonwealth Agricultural Bureaux, 1959.





FIGS. 1. and 2. Nests of *Oecophylla smaragdina* having sexual forms in them.

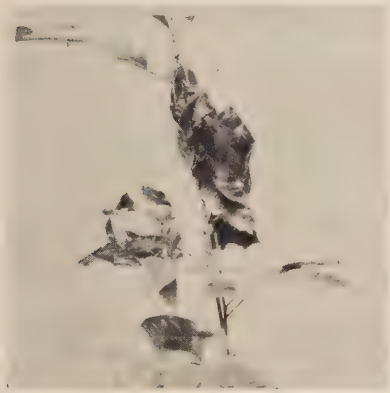


FIG. 3. Small nest of *O. smaragdina* having no sexual forms in it.



FIG. 4. Nest of *Crematogaster dohrni.*



FIG. 5. Nest of *Crematogaster* sp.



FIG. 6. Nest of *Polyrhachis affinis.*

FIELD TRIALS OF THE CONTROL OF *GLOSSINA PALPALIS* (R.-D.) BY OBSTRUCTIVE CLEARING.

By R. J. Kernaghan and J. B. Davies

Sleeping Sickness Service, Northern Nigeria.

(Plate XI.)

Nash & Page (1953), as a result of their studies on the ecology of *Glossina palpalis* (R.-D.) in Northern Nigeria, suggested a possible method of control, to be known as ' obstructive clearing '. The aim of the new technique was to obstruct the flight of *G. palpalis* and deny it the benefit of an insulating top canopy of vegetation, a necessary constituent of favourable habitat. It was realised that there would be a minimum degree of vegetation density which could be so treated, and that, on a large scale, obstructive clearing might have to be interpolated with normal ' partial clearing '. The suggestion was also made that the method might be used to prevent access by tsetse to individual village watering places, *i.e.*, as a protective measure in the way that short ruthless clearings were formerly used.

In late 1953, the West African Institute of Trypanosomiasis Research (W.A.I.T.R.) commenced experiments in a selected site, to determine the value of obstructive clearing (Nash & Steiner, 1957). The first experiment involved an obstructed length of river of 2 miles, and the second, a length of $1\frac{3}{5}$ miles. In both cases isolation of the sites was obtained by ruthless barriers, before obstruction of the experimental stretches was begun.

The control of *G. palpalis* in Northern Nigeria is a function of the Sleeping Sickness Service, in view of its importance as one of the two vectors of *Trypanosoma gambiense*. This Service was therefore interested in possible new methods of control, but was of the opinion that field trials on a larger scale than the W.A.I.T.R. experiments were necessary before the method could be accepted. As the need for a cheaper method of control was urgent, it was accordingly decided to carry on with field trials, without waiting for the final outcome of the W.A.I.T.R. experiments. However, it was not until early 1955 that the first trial was carried out, followed by the second trial in 1956–57. The delay was caused by the difficulty in finding suitable sites: a certain amount of selection had to be done in order to give the method a fair chance, while another governing factor was that it was essential, for financial and staff reasons, to fit in trial sites with existing schemes for the control of *G. palpalis*. The location of the two sites is indicated in fig. 1. It will be seen that there is a considerable difference in their latitudes, the first trial being in the Northern Guinea Savannah, near the north-western edge of the central Bauchi Plateau, while the second trial was much farther south, near the southern limit of the Southern Guinea Savannah zone. (Vegetational zones after Keay (1949).) In both cases, a population of *Glossina tachinoides* Westw. was associated with *G. palpalis*, but in such small proportions as to have no influence on the main findings.

The field trials were designed not so much to test the theory of obstructive clearing, which would be done by the W.A.I.T.R. experiments, as to discover the factors, if any, limiting its large-scale application and to devise practical methods of achieving the desired result. The W.A.I.T.R. experiments did not involve any partial clearing, although the possible results of mixing partial and obstructive clearing were a matter for some argument. They also made no test of the

suggestion that access by tsetse to individual village watering places might be prevented. This suggestion implied that obstructive clearing would in itself constitute a barrier, a result which if realised would be one of the most attractive features of the method. The first trial was therefore not isolated by barrier clearings before obstructive clearing commenced, although a terminal barrier was later inserted, while it included a trial, remote from the main scheme, of obstructive clearing used protectively. The second trial site was isolated by barriers, in response to criticism of the first trial, although known possible sources of fly reinvasion into the obstructed area ('reservoirs') were left within the isolated area. The two trials were therefore not replicates of each other, and must be considered separately. In addition, different staff was employed in the two trials, each developing its own technique in bringing about obstruction. Taken together, therefore, the two trials explored a number of aspects of practical importance not covered by the first experiments.

The present authors prefer the term 'obstruction' to 'obstructive clearing' since 'clearing' implies removal of vegetation, which is not done (officially). In point of fact, however, it did so happen that so much of the obstruction was removed by the local people, or destroyed by floods, that the streams came to have the appearance of having been partially cleared. 'Obstructive clearing' was therefore not such a paradox as at first it seemed, but for reasons which were not apparent when the term was coined. It is important to note that when the expression "obstruction of the (stream- or) river-bed" is used in this context,

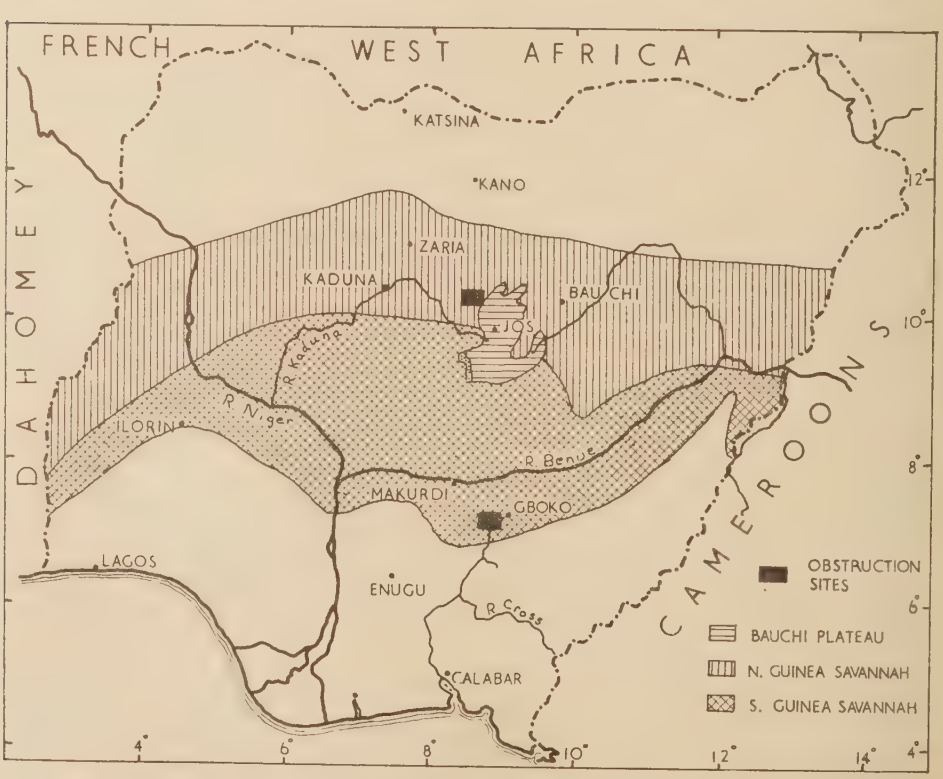


Fig. 1.—Outline map of Nigeria showing location of obstruction sites and relevant vegetation zones.

no deliberate impediment of the natural flow of water is implied. It refers only to the space, between the banks, above the *normal* water level, which is the flight line of the fly.

The First Field Trial.

Description of the site.

The headwaters of a stream, the River Bunu, in Lere District, Zaria Province, were selected for the first field trial (fig. 2). The area comprises typical Northern Guinea Savannah zone woodland, considerably interspersed by native farmland. It lies towards the north-west side of the central Bauchi Plateau, and granitic outcrops are common, in places rising to form prominent inselbergs. The streams arise as drainage depressions, but quickly acquire a well-marked bed 5–10 ft. deep, and a characteristic vegetation of riverine species. These include *Uapaca somon*, *Berlinia heudelotiana*, *Khaya senegalensis*, *Syzygium guineense*, and *Adina microcephala*. The latter species is often associated with a shallow, rocky stream-bed, the banks of which are usually low, and devoid of any other vegetation. Smaller trees include *Phoenix reclinata*, *Raphia sudanica*, *Garcinia ovalifolia*, and *Oxytenanthera abyssinica*, with *Landolphia* sp. and *Mucuna pruriens* as common climbers.

The main stream and its tributaries gave a length of nearly 13 miles suitable for obstruction before the stream-bed became too wide, and the associated vegetation too sparse, for efficient blocking. This unsuitable stretch of river ended at a large rock outcrop, completely devoid of any vegetation. After passing this rock, the narrow stream-bed with its typical vegetation was resumed, and it was in this neighbourhood, some miles farther downstream, that the trial of the protective value of obstruction was carried out.

The watershed of the selected system of streams gave reasonable natural isolation, so that the main danger of reinvasion by fly came from the uncleared main stream, below the trial site. Nomadic Fulani cattle were grazing over the area at the time the obstruction was carried out. This was a complication which had to be accepted, and of which the true significance has never been fully evaluated. It is thought likely that they may attract both *G. palpalis* and *G. tachinoides*, and may even transport them across watersheds; while Nash & Steiner (1957) point out that they may provide a source of food at a time when the natural hosts have been displaced by clearing activities, etc.

Method.

After surveying by compass traverse, the stream system was divided into sections of 100 yd. by a series of numbered pegs. In addition, definite points (12 in number, later increased to 13) were demarcated at places where there was a favourable habitat for *G. palpalis*. Four of these were downstream, beyond the proposed limit of obstruction, though one of these was later included in a ruthless barrier clearing (fig. 2). Two methods of assessing the tsetse population were used—day catches at the fixed points, repeated twice a month, and patrols over the whole area, so arranged that complete coverage was given once a month. All tsetse caught on these patrols were referred to the nearest peg number. Fixed-point day catches (9 a.m.–3 p.m.) are considered to be more useful than normal fly-rounds in dealing with riverine tsetse, particularly when the fly density is low (as it usually is, in Northern Nigeria) and not of uniform distribution. In both cases, caught flies were released at the end of the day, to avoid depopulation.

Obstruction was carried out at the extreme end of the dry season (completed by the end of April), when maximum concentration of fly could be expected in the stream-beds. Unfortunately, it was not possible to carry out lengthy pre-obstruction observations; post-obstruction observations were carried on for 17 months. It is not proposed to give in detail the technique employed in bringing

about obstruction in either this or the second field trial. In both cases, efficient methods and organisations were devised by the respective officers in charge, differing between themselves and from that laid down by Nash & Steiner (1957). It suffices to say that the resulting obstruction was, by personal observation, as good as that of the original experiments. The various streams usually had to be ruthlessly cleared for 200–300 yd. from their sources, until a sufficiently definitive stream-bed had been formed to allow obstruction. The associations in which *Adina microcephala* was dominant did not permit obstruction, due to the sparseness of other vegetation, and the shallow nature of the stream-bed. They were usually of limited extent, and were partially cleared.

One aim of this trial was to test the theory that if obstruction was so unfavourable that a tsetse population within it was eliminated, then it should inhibit immigration into it of tsetse from outside or, at any rate, neutralise them. In other words, it should constitute a tsetse barrier. To this end, the terminal point

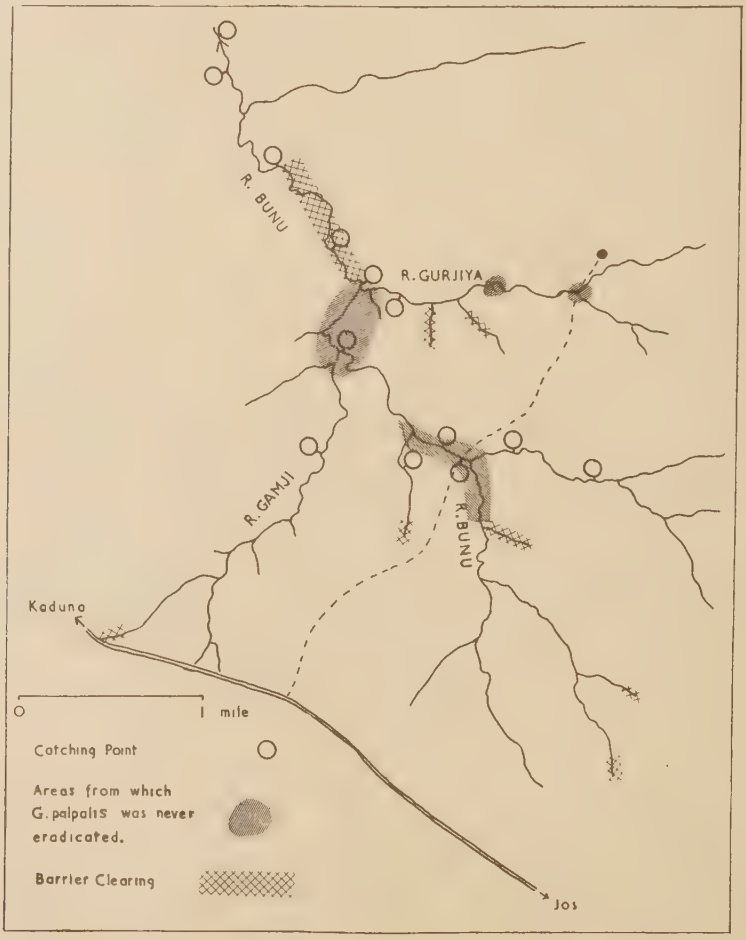


Fig. 2.—Site of the first field trial. 'Barrier clearing' includes the terminal barrier and also the sections of river impossible to obstruct and therefore ruthlessly cleared.

of the obstruction, downstream, was left abutting on undisturbed tsetse habitat that supported a reasonable population of fly. A ruthless barrier was inserted at this point, 11 months later, cutting off this source of immigrant flies. Thereafter, if any fly population, originally present, declined, it would indicate that obstruction had a lethal effect, but if not, the fly population could be presumed to be truly resident.

Altogether, 11⅓ miles of stream were obstructed, while 1¼ miles were either ruthlessly or partially cleared. This latter was not costed separately, owing to its piecemeal nature. The total cost worked out at 370 man/days per mile, which compares favourably with the figure of 390, quoted by Nash & Steiner (1957) for obstruction only. Normal partial clearing in this area usually averaged 600 man/days per mile.

After obstruction had been completed, very satisfactory thickening-up of the vegetation took place. Creeper growth, particularly of *Mucuna pruriens*, became well established, supported by the débris of the fallen trees, so that the river-bed became impenetrable (Pl. XI, fig. 1). There was naturally a tendency for the original mound of trash to sink into the bed, as some of the supports gave way.

One of the first criticisms of the theory behind obstruction was the possible effect of an increased water flow on the obstruction (or *vice versa*). This was answered in no uncertain manner, six weeks after the completion of obstruction, when the first heavy storm of the wet season occurred. The River Bunu rose in spate and the central section of the obstruction was wrecked for 2½ miles. Large trunks, which had formed main supports for the new creeper growth, were deposited high on the banks, but the most noticeable feature was the formation of dam-like barriers of débris, several feet high, across the river-bed at intervals of 20–50 yd. The intervening spaces were left completely open, and after a few weeks of normal regeneration, the general effect was similar to that produced by 'bad' partial clearing. (Pl. XI, fig. 2.) Subsequently, 1½ miles of the River Gurjiya obstruction were similarly wrecked. The other tributaries remained obstructed.

It is considered that this phenomenon was due to the affected tributaries acting as drainages to catchment areas of more or less bare rock, in the form of outcrops and low hills. There was little ground absorption, with the result that the entire precipitation went immediately into the streams. The net result was that four miles of very promising obstruction was disturbed, unfortunately including the sections with the highest fly density. Consideration of the occurrence after the event leads one to accept it as a hazard natural to the area, rather than a freak, although at the time it was completely unexpected, being previous to the suggestion made by Nash & Steiner (1957) that, under circumstances similar to the above, the obstruction is likely to be displaced.

Data and results.

As already mentioned (p. 451), data on the fly population was obtained by two methods—day catches at fixed points, which commenced previous to the obstruction, and patrols over set sections of river, in which flies were caught at random, the point of capture being referred to the nearest numbered peg. These patrols were not commenced until after obstruction had been completed, when it was felt that the criticism might be offered that the fixed points did not give representative coverage. In point of fact, the patrols proved the good initial siting of the fixed points and added little to the information provided by the latter.

The picture presented by the initial data was typical of the area for the season (late dry season)—a population of *G. palpalis*, low in absolute numbers and diffuse but with a tendency to concentrate at favourable sites along the main stream. The upper reaches of the tributaries, which were to lend themselves most readily

to obstruction, supported an extremely low population. This was to be expected, following Nash & Page (1953), as their narrow width and high banks, with numerous meanders already partly occluded by vegetation, did not fulfil the conditions for favourable habitat. *G. tachinoides* was present but in such low numbers as to be insignificant when standardised and plotted. It eventually appeared to die out, so that all results refer only to *G. palpalis*.

The results from the fixed-point catches are shown in fig. 3. The four points downstream, beyond the obstruction, were used as a control, leaving four points on the main-stream obstruction, and five on the tributaries. Data from these last nine points have been plotted (a) together, for the over-all effect, (b) separated into main stream and tributaries. Considering the obstruction as a whole, it will be seen that, after a fairly sharp initial drop, there was a gradual decline in the number of flies, a minimum being reached one year after. From then on there was a tendency for the population to increase. The population decrease was more emphatic on the tributaries, and, considering these alone, the obstruction may be considered to have been at least partially successful. On the main stream, however, it was evident that the fly population was still well established and, although it had suffered a set-back, was in a position to reach its former level.

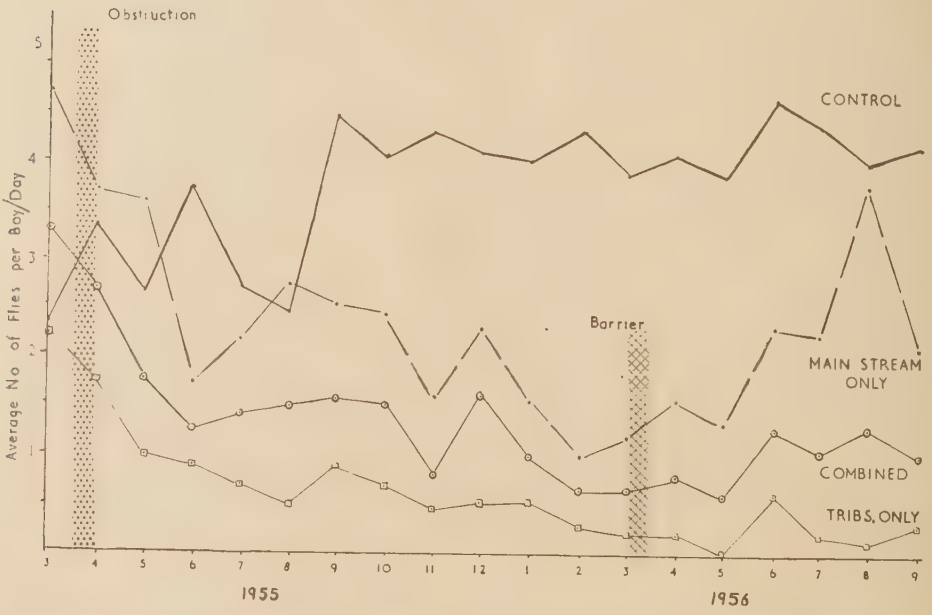


Fig. 3.—Comparison of catches of *G. palpalis* in control and obstructed sections. The catches in the main stream and the tributaries are plotted separately, and combined. The effect of the persistence of flies in the main stream on the total figures will be noticed.

Bearing in mind the low absolute figures, the ruthless barrier, cut eleven months after obstruction, appeared to have little or no effect. One control catching point was involved in the barrier. From then on, its catches were negative, and showed no indication of any crossing over from the end of the uncleared stretch into the obstructed reach. There was possibly a slight reinforcement of the population in the obstructed reach, due to flies being driven in when the barrier was cut, but there were already indications of a rising population in the previous month. The barrier was commenced from the end of the obstruction

and work proceeded downstream, so that flies would have tended to be driven away from the obstruction. There was no increase recorded at the end of the uncleared stretch, so it is not considered likely that any increase at the end of the obstructed stretch was significant.

The patrols at first yielded a few flies in the smaller tributaries but it soon became apparent that there was a permanent fly population existing in definite concentrations along the larger streams, from which there was little dispersal. These concentration sites are indicated in fig. 2, and coincide with areas that formerly constituted favourable habitats. The situation and extent of these sites shown in fig. 2 actually represent the final position after 17 months of observations, but there was little change throughout this period, and *G. palpalis* could be caught with certainty, in these areas, at any time.

The ' protective ' value of obstruction.

In order to test the suggestion (Nash & Page, 1953) that obstruction might be of value in preventing man/fly contact (*i.e.*, analogous to the early type of ' protective ' clearings at important points of man/fly contact), a trade-route crossing was selected, some miles away from the first field-trial site. The stream was obstructed for 300 yd. on either side of the crossing, as was a tributary which joined the main stream at this point (fig. 4). Catching points were established

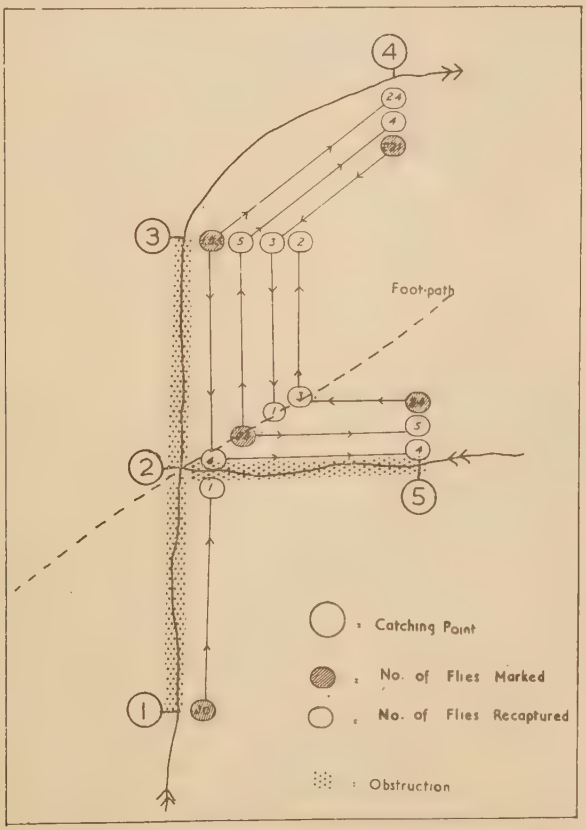


Fig. 4.—Diagram of the trial of the protective value of obstruction.

at the crossing and at each end of the obstruction, with a control point some hundreds of yards downstream.

The aim of the trial was to see if there was a maintained reduction of flies at the crossing, and to see if flies would move through the obstruction from the terminal points. Marking of flies was therefore carried out, commencing one month after obstruction had been completed. Observations were carried on weekly for 15 months after obstruction, although for unavoidable reasons no records were made for December 1955. The results are indicated in fig. 4. The catches at the crossing place (Point 2) showed a decrease and reached zero in the dry season, but then began to recover. In each of the last three months of observations no old flies, but only recent emergents, were caught, indicating an actively reproducing population in the vicinity of the point. Points 1 and 5 were somewhat anomalous in that the fly population appeared to die out. They were not particularly favourable habitats but it seems unlikely that the decrease was due to any of the effects of obstruction, and that other factors were at work.

The marking of flies showed that there was movement either through or along the obstruction. There was in some cases the possibility of movement across country, *e.g.*, from Point 1 to Point 5, but resources did not permit investigation on this. Whatever route was followed, it was evident that the centre point could be reached from the extremities.

TABLE I.

Recapture of marked flies in ' protective ' obstruction.

Point No.	Total flies marked	Recaptures at Points				
		1	2	3	4	5
1	20	—	1	—	—	—
2	74	—	14	5	4	5
3	195	—	4	29	24	4
4	221	—	1	3	25	—
5	84	—	3	2	—	23

The distribution of recaptured flies is shown in Table I. The arm of obstruction leading to Point 1 was unpopular. This could be due to the obstruction, but, as already pointed out, this was not originally a section of favourable habitat. However, it was often in such unfavourable sections that the best obstruction was obtained. Movement up and down the other obstructed arms was more evident, flies from both terminal points (Nos. 3 and 5) penetrating to the crossing, and then on to the opposite terminal. Flies from the control catching point were obviously reaching the crossing in small numbers, although the movement in the section of untouched river between the control point and the obstruction tended to be greater from the obstruction to the control than in the reverse direction.

The net result was that approximately 1·5 per cent. of all flies marked at the terminal obstruction and control points reached the crossing. Most movement took place in the wet season, but, even so, this figure is too high to give protection comparable to that given by normal protective clearings, into which there is remarkably little wet-season penetration.

This movement was no doubt responsible for some of the 74 flies marked at the crossing, but of these, approximately 20 per cent. were subsequently (*i.e.*, after a minimum period of one week) recaptured at the point of marking. Conditions at the crossing must therefore have provided reasonable existence for *G. palpalis* and opportunities for trypanosome transmission.

The Second Field Trial.

Description of the site.

The second field trial of obstruction was carried out in Benue Province, about ten miles south-west of Gboko and, as already pointed out, was situated towards the southern edge of the Southern Guinea Savannah zone. The riverine vegetation tends to be heavier than that encountered in the first trial, with frequent stretches of very wide high forest (up to 400 yd. on either bank) which is swampy for most of the year. The surrounding country is slightly undulating, and the rivers slow-running, dependent on the water-table rather than surface drainage for their water, so that no untoward effects due to rapid flooding could be expected.

This trial involved a sub-system of the River Konshisha, a tributary of the Cross River, consisting of a main stream (River Ategba) and several tributaries (fig. 5). On the main stream, 11 miles of obstruction were planned, with 18 miles on the tributaries. The River Ategba at its downstream junction with the River Nienga, is 15–25 ft. wide, with banks 4–6 ft. high. The vegetation, not particularly dense, consisted of a few tall emergents such as *Khaya senegalensis*, and an understorey of *Sterculia* sp., *Adina microcephala*, *Syzygium guineense*, and a few examples of *Vitex doniana*, with associated creeper growth of *Mucuna pruriens*. Proceeding upstream, this vegetation was constant to beyond the River Ayande II, although the stream had narrowed to 10 ft. in width, while the banks were only 3–4 ft. high. The banks then became very low and it was apparent that the stream overflowed very easily. The tall emergents remained, but the understorey was replaced by a dense thicket about six ft. high. After this section, the vegetation resembled that of the lower reaches, but with more thicket (mainly

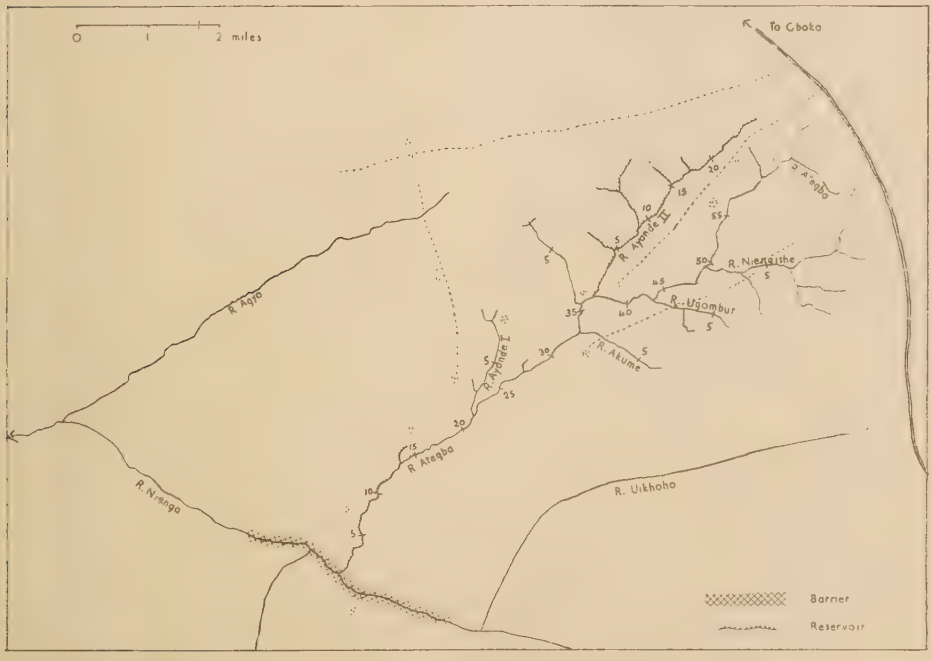


Fig. 5.—Site of the second field trial.

Alchornea cordata) and the stream itself narrowed down to six ft. in width, with banks 2–3 ft. high. With the exception of the River Ayande II, all the tributaries and the upper reaches of the River Ategba resembled each other, with vegetation similar to the upper main stream. They all had their sources in patches of forest, which were typically swampy, with numerous palm trees (*Phoenix reclinata* and *Elaeis guineënsis*) and *Uapaca* sp. These forest areas were normally about 100–150 yd. in width and extended for varying distances down the tributaries. The River Ayande II differed from the other tributaries in that it meandered through such forest for the whole of its length, its bed being ill-defined and subject to flooding at the slightest rise in the water-level. This forest was seldom less than 50 yd. in width on either bank, and in one place was 400 yd. wide on either bank.

Method.

The site was isolated from the main river system by cutting a ruthless barrier on the River Nienga, stretching for one mile on either side of the River Ategba junction. A separate tributary (R. Agyo) of the River Nienga was chosen as a control (fig. 5). The River Ategba and its tributaries were then divided into 300-yd. sections, to which the numbers in fig. 5 refer. As at that time there was no definite proof that the reduction in fly population caused by obstructing a river was due to the physical obstruction alone and not to the accompanying sudden loss of shade caused by disturbing the vegetation, 4,500 yd. (sections 1–15) of the Ategba were left undisturbed to act as a ' reservoir ' in order that flies could penetrate freely into the obstructed reach for some time after the work was completed, to take the place of any flies killed by the initial loss of shade caused by felling the trees. After a year, it was intended to obstruct the reservoir, thereby removing the source of invasion, and it would be seen whether any pockets of fly that had become established during the year could continue to exist in mature obstruction without reinforcement. However, it so happened that it was not possible to complete the whole of the obstruction programme by April 1956 as planned, so the River Ayande II was left to act as a second reservoir. Both reservoirs were obstructed early in 1957.

The cost of obstruction averaged 450 man/days per mile compared with normal partial clearing which would probably have been in the region of 1,000 man/days per mile. Good obstruction was obtained on the tributaries, forming a mound of trash which was still appreciable after one year. Creeper growth was vigorous and developed more quickly than in the first field trial. In the lower reaches, where the river was 15–20 ft. wide, the cut vegetation did not nearly fill the river. What there was, was quickly removed by the stream in flood and the depredations of the local people in their search for firewood, so that the ultimate result resembled ' bad ' partial clearing. In wide patches of forest, it was not possible to drag fallen trees 150 yd. or so to the stream, without considerable effort and expense. Consequently they were left where they fell, in the hope that all the forest area would be converted into an impenetrable thicket, and therefore intolerable for *G. palpalis*, which normally ranges with complete freedom throughout such forest. In practice, this was not achieved as regeneration from such species as *Uapaca* sp. and *Ficus* sp. broke through the mass of débris, to form possible small localised habitats.

In places the vegetation was insufficient to produce continuous obstruction, while elsewhere, on the water subsiding at the end of the wet season, the creeper growth was found to have formed an arch over the stream, forming a possible flight line for the fly beneath. The forest areas at the sources of the streams were denuded fairly thoroughly as the local people took advantage of these obstructed marshes to grow rice and, in so doing, removed all the remaining vegetation, leaving them completely open.

Fly data and results.

Shortage of staff did not permit all of the 29 miles of the system to be covered by comprehensive fly-rounds. Instead, a programme was devised whereby most of the stream would be visited once a week. Catching points corresponding to the numbered sections were established, 50 points being on the River Ategba (a continuous stretch of over 8 miles), 15 points on the River Ayande II, and points on the lower five sections on each tributary. Two catchers spent half an hour at each point. As there were two teams, each team visited alternate points in order to minimise any difference in catching ability between the teams. For record purposes, each five points were grouped together, representing 1,500 yd. of stream, and catches were recorded as the average number of flies caught per visit each month, per 1,500 yd. On the control stream, five points were selected, and visited similarly.

The initial population was of mixed *G. palpalis* and *G. tachinoides*, with the former very much predominating. The catches of *G. palpalis* and *G. tachinoides*

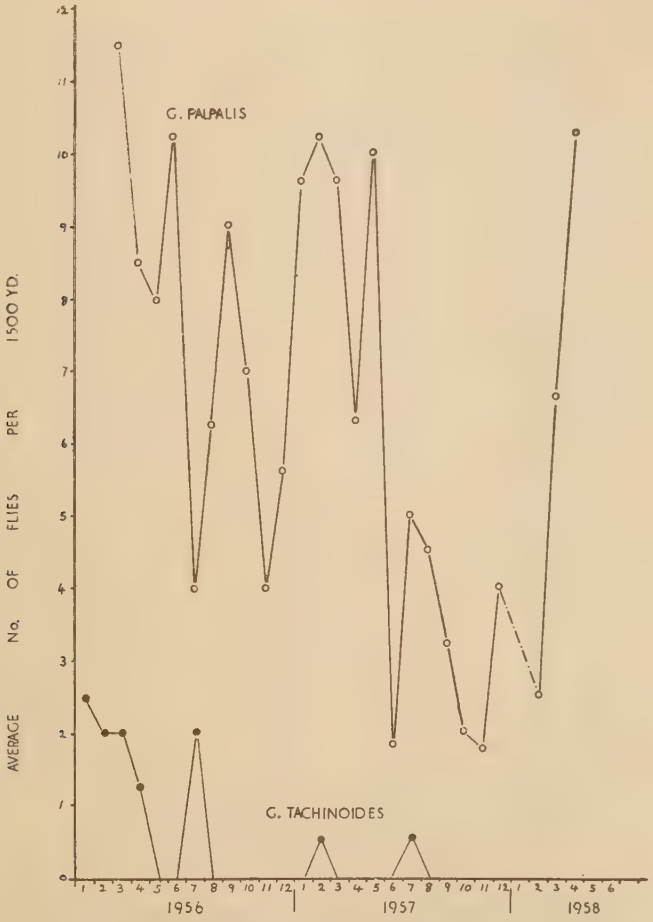


Fig. 6.—Comparison of catches of *G. palpalis* and *G. tachinoides* on control stream.

on the control stream are compared in fig. 6. These were representative of the *palpalis/tachinoides* ratio over the whole area. It will be seen that the small population of *G. tachinoides* present in January 1956 decreased during the year, only reappeared on two occasions in 1957, and not at all in 1958 (to date). Consequently, although the figures given in fig. 7 include both species, in reality they represent only variations in the population of *G. palpalis*. The last example of *G. tachinoides* caught in the obstructed reach was in January 1957, but as this species had also disappeared in the control, this can hardly be attributed to the obstruction. It was never considered likely that the method would be of use against *G. tachinoides* (Nash & Page, 1953), although it also disappeared in the first trial. In both cases, it is near the limit of its distribution, and, under such conditions, does seem liable to sudden fluctuations, for reasons not yet explained.

The overall effect of obstruction on the fly population is shown in fig. 7. Although the obstruction was commenced at a time when the population was

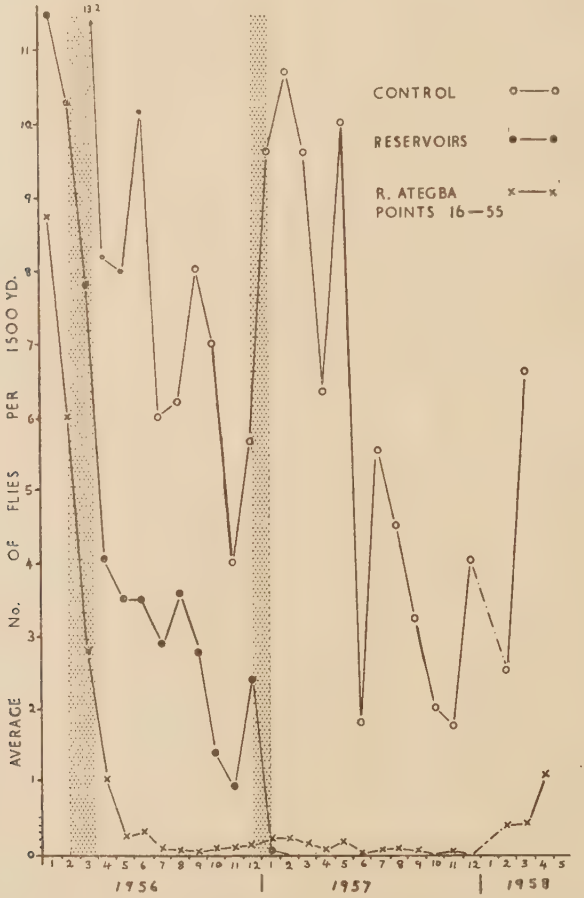


Fig. 7.—Comparison of catches on the control river, R. Ategba (main stream) and in the reservoirs. The stippled areas indicate the periods when obstruction of the main stream and the reservoirs, respectively, was carried out.

falling, it obviously had a marked effect, which was repeated in the reservoirs when they were obstructed. These showed a complete disappearance of population, with no subsequent recovery. Unfortunately, the main stream never showed complete eradication along its whole length, flies continuing to exist in small numbers, in certain well-defined areas, in particular between points 33–35 and 50–53.

The catches on two adjacent 1,500-yd. stretches of stream are compared in fig. 8, which demonstrates this localised distribution. After obstruction, points 31–35 showed a low persistent population which eventually began to rise early in 1958, while flies disappeared from points 26–30, though they reappeared in April 1958, 22 months later, probably due to reinvasion from upstream. There was complete eradication on the tributaries.

Tests of fly movement were tried by marking, but the number of recaptures was very small. However, these did indicate that movement did take place up

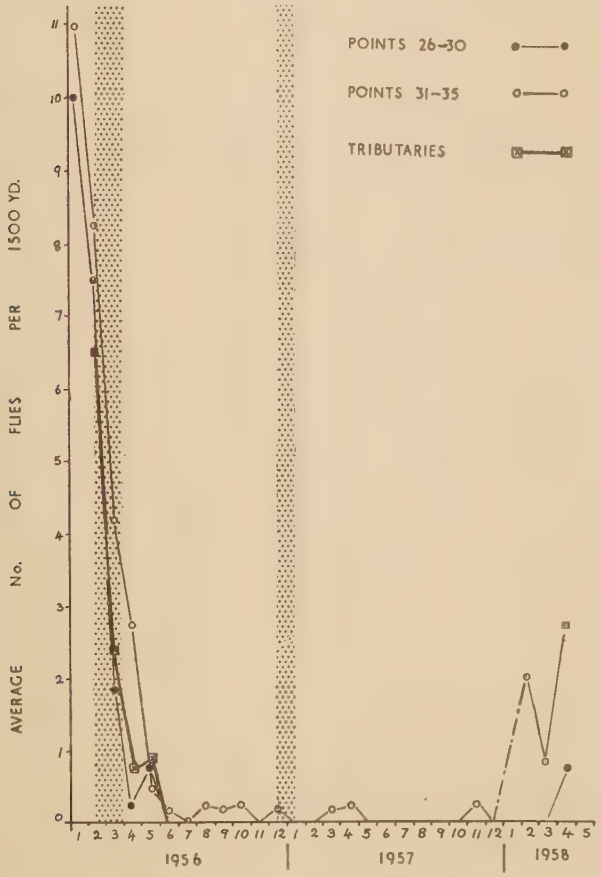


Fig. 8.—Comparison of catches on two adjacent 1,500-yd. stretches of the main stream and on the tributaries, indicating the localised distribution of the residual population. The stippled areas indicate the periods over which the two stages of obstruction were carried out.

and down the obstructed reach. For example, one fly travelled 3½ miles from the point of marking in two weeks. When obstruction commenced, working upstream from the first reservoir, an initial slight increase in the reservoir population was noted, indicating that flies had been driven in from the obstruction. From then on, marked flies from this reservoir were occasionally found up to 1,500 yd. up the obstructed reach, but no large-scale immigration was noticed. There was no evidence that any movement into the obstructed reach took place from the Ayande II reservoir. One fly from the obstructed reach was recaptured some way up the reservoir, a direction of flight which was to be expected. During 1957, flies marked in the obstructed reach of the main river were repeatedly recaptured two months or so later in the same location, showing that, at the points already mentioned in the preceding paragraph, they were well established. It is to be expected that, after two years, regeneration of the larger more important species in the vegetation should become appreciable along most of the obstructed stretches, while the effect due to the obstruction may have become negligible. Conditions are then becoming suitable for dispersal of fly from the persisting foci to other sections (*e.g.*, nos. 26–30), as was noticed in April 1958.

Discussion.

From the foregoing account of these two field trials of obstruction it will be seen that, although in different areas and under different supervision, their results had a certain amount in common with each other. Neither can be considered successful, as there was not complete elimination of *G. palpalis*, but undoubtedly the fly population did receive a great set-back, which amounted to elimination in the minor tributaries. It is often doubtful, however, if these latter are important habitats, by virtue of their already occluded nature, although of course they are usually the easiest to obstruct.

Obstruction has been proved to be of no value in limited 'protective' schemes, a significant number of *G. palpalis* reaching the centre point from the unobstructed ends. On the other hand, there was remarkably little penetration from the fly reservoirs into the obstructed reach in the more extensive trials—no more than one would expect into a barrier clearing. (Nash & Steiner (1957) demonstrated the crossing or circumvention of a barrier, one mile long.)

It is considered that the main objection to the wide-scale application of obstruction as a means of controlling *G. palpalis* is the difficulty of ensuring that a high enough degree of obstruction is achieved and maintained throughout, without patches of imperfect obstruction either being left or arising later. The latter may be due to a number of causes. Obstruction that is apparently good may prove to be unsatisfactory for intrinsic reasons difficult to define, their effect only being noticed by continual fly-rounds. On the other hand, definitely good obstruction may be subsequently broken down by obvious extrinsic causes. There is a danger, therefore, that:—

(a) habitable sites may be left, or may quickly develop, affording refuge to individuals of the original population. (In this connection, the question of possible adoption of atypical habitats must not be overlooked. This has been noticed with *G. tachinoides*, but not with *G. palpalis* as yet.)

(b) refuge may be offered to immigrant flies.

In these two trials (a) above is considered to have been of much greater importance than (b), flies finding it possible to live for at least two months on stretches of imperfectly obstructed stream even in the dry season.

Apart from the stretches of river which show possibilities for obstruction there are the sections which are obviously impossible to obstruct. Experience shows that it is unusual to find long stretches of good potential obstruction without their being interspersed with these sections that cannot be obstructed, which become more and more continuous as the river broadens, or as the width of riverine forest

increases. In such cases, resort would have to be made to partial clearing, and the advantage of the lower costs of obstruction, its main attraction, would not be gained in the places where it was most desirable, *i.e.*, on the larger rivers, the cost of clearing which is becoming so formidable. It is therefore felt that there would be no great advantage in carrying out obstruction unless it could be the dominant technique throughout the area in question.

Complementary to the above, field-trial experience enables a number of factors limiting the wide-scale application of obstruction to be stated:—

1. The dimensions of the river-bed. If the width is over 10 ft., and the depth greater than 6 ft., there will not often be sufficient vegetation to fill it over long distances in such a way as to obtain successful obstruction.
2. The presence of wide riverine forest, often swampy, through which *G. palpalis* ranges freely and without being so dependent for its survival on the river-bed as where the riverine vegetation is more limited.
3. The rate of run-off of water in the catchment area. This is more important than the total rainfall, and is obviously connected with the topography and geology of the immediate area. It will act in opposition to conditions favourable under 1, above—the narrower the river-bed (*i.e.*, the more suitable for obstruction) the greater will be the disruptive effect of the water in spate.
4. The presence of certain plant associations in the riverine vegetation, and their edaphic relationships. For example, *Adina microcephala* usually indicates a rocky bed with low eroded banks practically devoid of any other vegetation, and impossible to obstruct adequately.
5. The difficulty of preventing human interference with the obstruction; *e.g.*, vital constituents of the obstruction may disappear, in the form of firewood. (This may have been aggravated in the second trial by the access given to the river by the fly-round paths, which had to be maintained, but which normally would not be present.)

No difficulty was found in devising satisfactory techniques of obstruction, and the saving in labour costs over normal clearing was from 40–50 per cent. An original criticism was that junior supervisory staff might be confused by the somewhat contradictory nature of the new method, when being used along with the established method. In the trials, this did not happen, as the amount of partial clearing was small, while senior supervision was close, but in a later attempt to use obstruction as an adjunct to a partial-clearing scheme, confusion did arise. The result was an unfortunate combination of both methods, all the vegetation being cut and carefully deposited on the banks, after which it was thrown back into the river-bed, at a cost considerably greater than partial clearing alone.

The limiting factors outlined above involve much more comprehensive survey work than is normal for partial clearing. The results of these surveys, which are expensive and time-consuming, may still indicate the unsuitability of obstruction. The difficulties encountered in finding suitable trial sites have been mentioned at the beginning of this account. The difficulty of ensuring perfect obstruction over long stretches of river has already been stressed. In fact, it seems that one could not be absolutely sure of success without very detailed follow-up fly-rounds carried on for a considerable period. It will be seen, therefore, that an obstruction scheme would need considerably more pre- and post-operational work (particularly the latter) than a corresponding partial-clearing scheme. This would entail a longer commitment of staff and the consequent limiting of tsetse control activities which would negative any advantages derived from the use of obstruction.

The possible 'repair' of broken-down obstruction is a point that has never been considered. In the case of the present trials, the first has been abandoned, while the second, being in an area where tsetse control operations are still being

carried out, will have its residual fly population eradicated by the use of insecticide.

The actual reason for the decrease in the population of *G. palpalis* remains unknown. It may be due to the physical difficulties imposed by the obstruction itself, or to the removal of the closed canopy. There is perhaps more to be said for the latter. The unanimous opinion of experienced tsetse-control officers who saw the trials was that obstruction, as a result of various extrinsic agents working upon it, came to resemble 'bad' partial clearing. 'Good' partial clearing involves removal of all trunks and débris from the river-bed, the burning of all trash over the stumps of the larger trees to discourage regeneration, and the removal of all minor stumps. The aim is for grass cover (or cultivation) to succeed the original vegetation, which is represented only by the former emergents. Probably about 50 per cent. of the cost of partial clearing is absorbed by this 'tidying-up' process, the degree of which is the criterion that determines whether a clearing is 'good' or 'bad'. The fact that, under certain conditions, obstruction is degraded to resemble badly finished partial clearing and still remains free from fly for much of its length, tends to suggest that the partial-clearing technique is perhaps too meticulous. The logical extension of this idea is what might be termed 'destructive' clearing (to add to the already numerous varieties of clearing), in which the trees would be left as they were felled. It seems possible that either some sort of obstruction would develop, or removal of the débris would take place, leaving open river banks. In this connection, it may be noted that, a number of years before the obstruction theory was put forward, it was observed that old protective clearings in the area of the first field trial, which had originally been badly done (*i.e.*, trees left as they fell, etc.) and subsequently neglected, were badly grown over, with luxuriant creeper growth. They were, however, remarkably free from *G. palpalis*, which presumably may now be explained, in the light of our present knowledge, by the obstructed nature of the stream-bed.

Such a method, although having some of the defects of obstruction (*e.g.*, the possibility of patches of suitable habitat being left), would probably have a wider application, with the same advantage of a much lower cost than normal clearing. However, further extensive trials would be necessary. These are not at present contemplated.

The conclusion drawn from the results and experience gained from these two field trials, indicating that success depends to too great an extent on a number of specialised conditions being satisfied, is that obstruction is unlikely to be used as a normal method of control of *G. palpalis* in Northern Nigeria. Whether, on a large scale, it would be more successful in vegetational zones other than the Guinea Savannahs, remains a matter for further trial.

Summary.

Two field trials of obstruction ('obstructive clearing') as a means of control of *Glossina palpalis* (R.-D.) in locations representative of the Northern and Southern Guinea Savannah zones of Nigeria, are described.

In neither case was complete eradication achieved, pockets of *G. palpalis* remaining from the beginning at certain points on the main stream. Greater success was obtained in the smaller tributaries, which lent themselves more to obstruction. There was little penetration of *G. palpalis* for any great distance into obstructed reaches from natural 'reservoirs' left abutting on to the obstruction, but a trial of the 'protective' value of obstruction failed, owing to complete penetration in some strength of 300 yd. of obstructed stream on either side of the point to be protected. In neither case was immigration of flies from elsewhere into the trial areas an important factor. Although, at first, the surviving fly

population was very localised, there were later indications that dispersal was beginning to take place.

Some accidents which may happen to obstruction are described, with their effects on its ultimate appearance. Consequent to these, a number of factors which limit the wide application of obstruction are stated. The more important of these are: the dimensions of the river-bed, which may be too large to permit of successful obstruction; the presence of wide swampy forest through which *G. palpalis* ranges freely; alternatively, the presence of shallow rocky stretches with low eroded banks that may be devoid of all but certain characteristic trees, where adequate obstruction is impossible; the rate of run-off of water in the catchment area, rapid run-off leading to spates which disrupt the obstruction; human interference with the obstruction in quest of firewood.

No technical difficulties were encountered in carrying out obstruction, and costs were from 40 to 50 per cent. cheaper than comparable partial clearing.

Considering the subsequent appearance of originally obstructed stream, and its frequent resemblance to partial clearing, the suggestion of ' destructive ' clearing is put forward, in which the top canopy would be destroyed, but no effort made either to create obstruction or to clear away the fallen trees. Instead, reliance would be placed on the action of the various agencies encountered in these trials, which brought about the disruption of the obstruction, to produce the desired end-result.

It is concluded that successful obstruction depends too much on specialised conditions, difficult to fulfil in large-scale tsetse control schemes, and that it is unlikely to become a normal method of control of *G. palpalis* in the savannah zones of Nigeria.

Acknowledgements.

Our acknowledgements are due to the Ministry of Health of the Northern Region of Nigeria for permission to publish this paper, and, in particular, to Mr. A. C. Rippingham and Mr. R. G. S. Crawford, of the Sleeping Sickness Service, who were, respectively, responsible for the carrying out of these two field trials.

References.

KEAY, R. W. J. (1949). An outline of Nigerian vegetation.—52 pp. Lagos, Govt. Printer.

NASH, T. A. M. & PAGE, W. A. (1953). The ecology of *Glossina palpalis* in Northern Nigeria.—*Trans. R. ent. Soc. Lond.* **104** pp. 71–169.

NASH, T. A. M. & STEINER, J. O. (1957). The effect of obstructive clearing on *Glossina palpalis* (R.-D.).—*Bull. ent. Res.* **48** pp. 323–339.

© Commonwealth Agricultural Bureaux, 1959.



FIG. 1. Undisturbed obstruction, six weeks after cutting. The good mound of trash should be noted.



FIG. 2. The effect, on obstruction, of a river in spate. These transverse 'dams' were formed at 20- to 50-yd. intervals, leaving uninterrupted river-bed in between.

BIOLOGY AND ECOLOGY OF THE GARDEN CHAFER, *PHYLLOPERTHA HORTICOLA* (L.).

VI.—THE FLIGHT SEASON: REPRODUCTIVE STATE OF FEMALES.

By A. Milne *

School of Agriculture, King's College (University of Durham), Newcastle upon Tyne.

The general aspects of the flight season of *Phyllopertha horticola* (L.) were described in Part IV of this series (Milne, 1958). The outstanding mass features are the two roughly equal and half-overlapping Phases: Phase 1, the swarming of the beetles over the grass sward, followed by Phase 2, the swarming on the surrounding bracken, hedges and trees. The sex proportions in the two Phases were examined in Part V (Milne, 1959). The present Part deals with the reproductive state of females in the same manner. (Reproductive state of the male was not investigated beyond ascertaining, by experiment and field observation, that he can copulate immediately on first emergence above ground, copulates frequently throughout his life, and seems to be fertile almost to the end).

Methods for Studying the Reproductive State.

At ecdysis, in the hibernation cell, the abdomen of the female is crammed with fat-body and there are no gross signs of eggs in the two sets of six ovarioles ("at most one oocyte is visible as a small swelling at the base of each ovariole," Laughlin, 1956). When the female arrives at the base of the sward, however, about six days later (Milne, 1956), considerable development has already taken place in the reproductive system. From this stage onwards, the present study was made on preserved material. Females were dropped into Pampel's Fluid immediately on collection, *i.e.*, not kept crowded in collecting tubes until moribund, but killed when vigorous. In this way the abdominal contents were very satisfactorily fixed and preserved. Dissections were made from one to six months after collecting, thus: The abdomen was cut off (including a small part of the thorax), put in water for a few minutes, laid on dry filter paper for a few moments to get rid of excess moisture, then opened in air under a low-power binocular microscope. The following four details were recorded.

(i) Amount of fat-body remaining.

Knowing the crammed condition of the abdomen at ecdysis, it was readily seen that females above ground in the flight season contain at most about half the original amount of fat-body and at the end of their life have none at all. The fat-body remaining was classified by visual inspection in four categories, *viz.*

Category	*Score*
None or merest traces	F.-B. 0
Very small amount	F.-B. 1
Medium amount	F.-B. 2
Fairly large amount (being *at best* no more than about 50% of the original full amount)	F.-B. 3

* Agricultural Research Council Unit of Insect Physiology.

This classification, though qualitative, was quite adequate for present purposes. For convenience, the categories were given the scores (arbitrary numerical values) shown, F.-B. meaning fat-body.

(ii) Kind and number of eggs.

Three categories—A, B and C—were recognised.

The ' A ' egg looks exactly like a newly laid egg. That is to say, the A egg is fully ovoid (or " prolate spheroid " according to Laughlin, 1956), 1·5 × 1·0 mm., with a brilliant white shiny surface.

The ' B ' egg has about the same volume as the A egg, but is neither ovoid nor white nor shiny. The B egg is either longer or broader; when longer it is rather like a straight slightly-flattened sausage in some cases and like a banana in others; when broader it roughly resembles a cylinder in some and a prism in others. It always has at least one dimple (this in the sausage and cylinder types) or one concave side (in banana and prism). It is dirty-white with a matt surface.

The B egg is in fact a full-sized but misshapen and discoloured egg. In fresh beetles *all* full-sized eggs are actually ovoid and white, but pressure with the side of a needle reveals differences in resistance to and recovery from deformation which are reflections of shell development. The end-effects of Pampel's fluid are clearly also reflections of shell development. With a fully developed shell the egg retains its shape and colour despite Pampel's fluid (A). When not fully developed the shell is such that the egg cannot withstand the stresses of its own partial dehydration and the pressures from general abdominal contraction caused by Pampel's fluid, and so becomes deformed and discoloured (B.). The preserving of females in Pampel's fluid therefore turned out to be a very efficient way of distinguishing between mature (A) and immature (B) full-sized eggs by mere visual inspection.

The ' C ' egg is like the B egg except that it is smaller and even more varied in shape. It ranges from just under half to about three-quarters of the full size. In shape it may resemble a sausage, a lozenge, a pyramid, a parallelopiped, a ball, etc., and is always somewhat irregular and dented. It hardly needs saying that the C egg is more immature than the B egg.

In addition to these three categories, there are usually some oocytes towards the bases of the ovarioles but these were ignored.

In effect, then, the classification means this: the A eggs are apparently ready for laying, the B eggs are certainly immature and the C eggs are still more immature.

(iii) Size of the bursa copulatrix.

The bursa is essentially an elastic bag into which the spermatophore is placed. In a virgin female it is small. With mating it becomes distended and may increase to as much as eight times the virgin volume (as seen in preserved specimens). Allowing for body size, the bursa was classified as small (S), medium (M) or large (L).

(iv) Gut contents.

The dissection provided most of the mid-gut and the whole of the hind-gut for examination. This was either empty throughout (E), or contained a little food (F), or was full of food (F+) or was filled to distension (F++). When the food is bracken the gut contents in preserved specimens are brick red, otherwise it is dark or brownish green.

As the fat-body dwindles and later as eggs are discharged, more and more abdominal space becomes vacant; this is taken up mainly by progressive inflation of the air-sacs, and to a less extent by distension of the gut with food.

Considerations in regard to Body Size.

Contrary to Raw's (1951) suggestion, large and small females do not differ as to length of life (Milne & Laughlin, 1956, pp. 15–16). Rate of reproductive development in relation to size was investigated as follows.

Twelve females were selected from a large random sample which had been collected as pupae in the field and then kept in a dark underground chamber. Six came from the extreme lower end of the sample weight-range and six from the extreme upper end. All twelve emerged from the pupal skin on the same day and each one was set up with a male in a separate mating jar on that day. Each jar contained 2 in. of fine soil topped by a quartered disc of turf. All the females were therefore of the same age and experienced the same conditions, including average temperatures rather higher than are met with in the soil in nature.

Seven days later, all the females were killed and dissected. The fat-body remaining was F.-B.2 in every case, which meant that development in the reproductive system was proceeding at the same rate in both the smallest and largest females in the population. An examination of the numbers of full-sized eggs in the two groups will confirm this (Table I). Egg-production is directly

TABLE I.

Full-sized eggs formed by the seventh day after emergence from the pupal skin: a comparison of the smallest and largest females in a population under laboratory conditions (see text).

Weight as pupa (mg.)	Eggs formed A + B	Weight as pupa (mg.)	Eggs formed A + B
151	11	195	14
152	14	197	12
154	9	197	15
154	10	198	13
155	11	199	16
155	12	199	16
921	67	1,185	86

proportional to body weight (Milne & Laughlin, 1956), and, therefore, if development is proceeding at the same rate, the ratio of eggs formed should be the same as the ratio of body weights, which in fact was so, *viz.*, 86/67 = 1·283 and 1185/921 = 1·286.

Since egg-production is directly proportional to body size, samples of females for comparison of their mean egg numbers at different times in the flight season must have similar size distributions. This condition was sufficiently met for the present broad purposes by always taking *random* samples from nature.

State on first arriving at the Base of the Sward.

On her way upwards from the hibernation cell, the female pauses for some time at the base of the sward before coming out on the surface (Milne, 1956). The condition of her reproductive system when she first arrives at the sward base has been studied experimentally in circumstances (see Milne, 1956, p. 34) closely simulating those she meets in the field. The results for seven females taken

randomly from a random sample of pupae are shown in Table II. The important points to note here are that 8·6 (6–11) full-sized eggs (A + B) have been formed, but only 1·3 (0–4) of these are ready to lay (A); and all individuals have considerable amounts of fat-body still remaining, mean score being F.-B. 2·7 (2–3).

TABLE II.

Reproductive state of females on first arriving at the base of the grass sward above the larval hibernation cells.

Individual female	Fat-body remaining (Score)	Eggs formed A	B	C
1	3	0	6	9
2	3	2	9	4
3	3	0	8	6
4	3	0	9	1
5	3	4	5	7
6	2	3	4	4
7	2	0	10	5
Range	2–3	0–4	4–10	1–9
Mean	2·7	1·3	7·3	5·1

Phase 1.

State on first arriving upon the Surface of the Sward.

The female normally stays about two days ($\frac{1}{2}$–4) at the base of the sward (Milne, 1956) but longer if the weather is then unsuitable (see Milne, 1959). When at last she comes out on the sward surface she is, of course, making her primary emergence into adult activity and, for convenience, is called a ' primary emerger '. In nature, one can be certain of having primary emergers only if collecting is confined to the first day on which females appear upon the sward. The dissection results from 31 individuals taken at random on the first female-day of seasons 1949–1952 are shown in Table III. Included also in the Table are 13 individuals (marked *) taken over the first ten days of seasons 1950 and 1951 but nevertheless known to be primary emergers because they came from caged turf from which all emerging beetles were removed daily (see Milne, 1959); as expected, these 13 individuals are closely similar to the 31 others in range and mean of eggs, and their proportions in the three fat-body categories are not significantly different ($\chi^2 = 3{\cdot}8$; $P = 0{\cdot}2$).

During the pause at the sward base, development proceeds (*cf.* Tables II and III) so that at primary emergence the female now has 12·9 (8–26) full-sized eggs of which 6·5 (0–20) are ready to lay, and the fat-body remaining has been reduced to a mean score of F.-B. 2·1 (1–3). Naturally, those individuals with least fat-body left have formed most eggs. The reduction of fat-body with progress in the manufacture of eggs is illustrated in Table IV.

There is obviously a considerable range of variation in the reproductive state of primary emergers. Thus some have no eggs ready to lay while, at the other extreme, some have nearly all their eggs ready. This variation has two sources. (1) Differences in individual behaviour: within limits, different females will feel

TABLE III.

Reproductive state of females at their primary emergence upon the sward surface above the larval hibernation cells.

Individual female	Fat-body remaining (Score)	Eggs formed A	B	C
*1	3	0	8	4
2	3	0	9	5
*3	3	0	11	2
*4	3	0	13	2
*5	3	1	8	2
*6	3	1	12	2
7	3	2	9	3
8	3	4	7	6
9	3	5	3	7
10	3	6	2	2
11	3	6	5	5
12	3	8	7	7
*13	2	0	11	3
14	2	3	8	7
15	2	3	9	6
16	2	4	4	8
17	2	4	6	5
18	2	4	7	10
19	2	4	8	4
20	2	4	8	5
21	2	4	9	2
22	2	4	9	5
23	2	5	6	3
24	2	5	6	8
25	2	5	8	2
26	2	7	5	5
*27	2	7	6	1
28	2	9	5	7
29	2	10	4	5
30	2	10	5	4
31	2	11	0	5
*32	2	11	6	7
33	2	12	2	5
34	2	14	7	4
*35	2	15	1	1
36	1	7	4	1
*37	1	7	7	2
38	1	9	4	10
39	1	10	3	2
*40	1	10	5	3
41	1	10	6	5
*42	1	11	8	1
*43	1	13	6	4
44	1	20	6	1
Range	1–3	0–20	1–13	1–10
Mean	2·1	6·5	6·4	4·3

* See mention on p. 470.

the urge for primary emergence at different stages of their manufacture of eggs. (2) The incidence of bad weather: a female may or may not be hindered from making her primary emergence for a greater or lesser time after she is ready to do so (see p. 470).

TABLE IV.

Reduction of fat-body with progress in the manufacture of eggs as evidenced by the reproductive state of primary emergers. (Summary of data in Table III.)

Number of females	Fat-body remaining (Score)	Mean eggs formed (and range)		
		A	A + B	A + B + C
12	3	2·8 (0–8)	10·6 (8–15)	14·5 (10–22)
23	2	6·7 (0–15)	12·8 (8–21)	17·7 (14–25)
9	1	10·8 (7–20)	16·2 (11–26)	19·4 (12–27)

State when Oviposition starts.

Having made her primary emergence, a female goes back into the sward before the end of mass activity on the same day. On the next occasion that she appears on the surface she is, of course, no longer a primary emerger. Hence, after the first day on which females appear and until all have made their primary emergence (achieved by 8–11 days before the end of Phase 1, see Milne, 1959), females seen on the sward are likely to be a mixture of primary emergers and individuals making their second or subsequent appearance.

Random samples of females were taken daily from the sward surface during activity throughout Phase 1 of the years 1950–1952. From the *second* female-day onwards in each season, these samples totalled 614 females of which 279 had some fat-body remaining and 335 had none (Table V).

TABLE V.

Reproductive state of females collected throughout Phase 1 of the years 1950–1952.

Fat-body remaining (Score)	Numbers of females	Mean eggs (and range)				
		A	B	C	A + B	A + B + C
3	69	4·9 (0–16)	7·0 (2–13)	4·6 (1–15)	11·9 (3–21)	16·5 (9–28)
2	135	9·9 (0–24)	4·0 (0–11)	3·9 (0–11)	13·9 (4–27)	17·8 (9–31)
1	75	14·7 (4–28)	2·5 (0–8)	2·1 (0–10)	17·2 (9–28)	19·3 (9–30)
0	335	6·9 (0–30)	0·5 (0–7)	0·7 (0–8)	7·4 (0–32)	8·0 (0–32)

It will be remembered (Milne & Laughlin, 1956) that in the laboratory the average female manufactures around 16 full-sized eggs in all before dying (mean from 644 individuals). Table V shows that the F.-B.1 individuals had on the average 17·2 (9–28) full-sized eggs (A + B). Among the 335 F.-B.0 individuals on the other hand, 46·0 per cent. contained neither A nor B eggs; 38·2 per cent. had 9 or more A + B eggs with a mean of 18·2 (9–32); and 37·3 per cent. had 9 or more A eggs with a mean of 17·6 (9–30). Clearly then, in nature (as in the laboratory), the female does not begin to oviposit until her fat-body is entirely

consumed and all layable eggs are matured. After consideration of the present data and the laboratory results of Milne & Laughlin (1956), it is concluded that the average female matures 16 or 17 eggs, with a range of 9–32.

Each fat-body score defines not a fixed percentage of original fat-body but a fixed *range* of percentage of it. Accordingly, there will be a range of reproductive development among individuals having the same score. On the grass sward throughout Phase 1, the eggs related to any particular fat-body score (F.-B.1, 2 or 3) *among females in general* are on the whole nearer maturity than those of known primary emergers with the same score. Thus in F.-B.1, for instance, the primary emergers have more C and B eggs, and fewer A eggs (see fig. 1). From

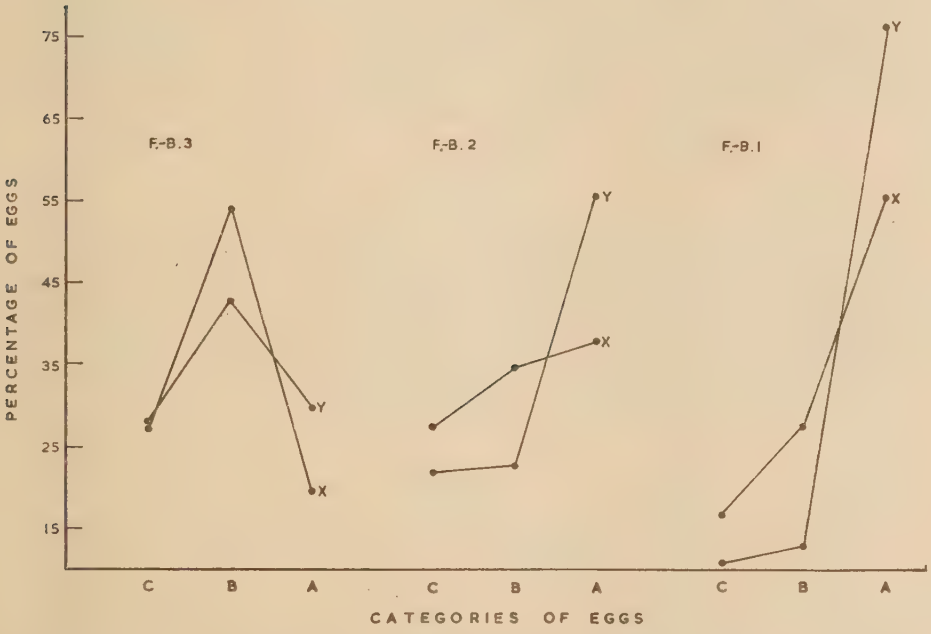


Fig. 1.—Proportions (percentages) of the three categories of eggs in females collected in Phase 1 and classified according to the amount of fat-body remaining. X, primary emergers alone (data from Table III); Y, all females with some fat-body, including primary emergers (data from Table V).

this it is evident that the average female reappears upon the sward on one or more days after her primary emergence before she begins to oviposit. And, obviously, the higher her fat-body score at primary emergence the oftener she will reappear.

The Bursa Copulatrix as Evidence of Copulation.

The size of the bursa copulatrix was noted for 342 of the 614 females taken throughout Phase 1. The data are given in Table VI.

One reason for measuring the bursa was a surmise that its size might give some idea of the number of copulations achieved by (and hence perhaps an estimate of the age of) any individual picked off the sward. A series of five experiments was made in which the mating of individual females was controlled.

The females were kept singly in culture jars with soil, turf cover and food. All were mated immediately on primary emergence; those in experiments 1–4 were not mated again; those in experiment 5 had 4–9 further matings spread more or less evenly over the period between primary emergence and death. All were killed, at the appropriate time, with Pampel's fluid, in which they were kept for

TABLE VI.

Size of bursa copulatrix and fat-body score in 342 females taken throughout Phase 1. (Relative sizes: S = small, M = medium, L = large.)

Fat-body remaining (Score)	Total females	Numbers of individuals with bursa			Percentage of individuals with bursa M or L
		S	M	L	
3	23	12	10	1	47·8
2	39	20	14	5	48·7
1	34	23	8	3	32·4
0	246	63	77	106	74·4

three months before dissection. The results are given in Table VII and prove to be quite wrong the surmise that the size of the bursa might give some idea of the number of copulations achieved by any individual picked off the sward. Comparison of experiments 5 and 2 shows that females with a large bursa could have had many copulations or only one. In view of this, the size must depend more on the presence of sperm than on the amount of sperm. One copulation makes little

TABLE VII.

Size of bursa copulatrix in relation to number of matings and time elapsed since first mating.

Experiment	Number of copulations per female	Time elapsing between sole or first copulation and death	Number of females with bursa size		
			S	M	L
1	1	0–2 hours	20	2	0
2	1	3–5 days	0	1	4
3	1	7–8 days	6	4	0
4	1	11–16 days	3	1	0
5	5–10	15–17 days	0	0	4

or no difference *at the time* to the size of the virgin bursa (see expt. 1); but in four or five days the bursa swells to the maximum size (see expt. 2). This swelling is caused by secretions of the bursa itself (Rittershaus, 1927) and perhaps by swelling of the disrupted spermatophore. The dwindling of the bursa to the medium or small size between the fifth and the sixteenth day, after a single copulation (see expts. 2–4), is due, at least in part, to the discharge of the spermatophore remains with perhaps some resorption through the walls of the chamber itself.

In the light of Table VII, Table VI is not entirely valueless. Even at the F.-B.3 stage, there are individuals with the bursa medium or large in size (Table VI). These must have been mated at least the day before (*cf.* expts. 1 and 2, Table VII), and this confirms the conclusion of the preceding section, namely, that after primary emergence the average female does not stay below ground but comes up again before oviposition starts.

State when Feeding begins.

In the daily random collections of females from the sward in Phase 1 (see Table V), there were 279 individuals with F.-B.3, 2 or 1 and 335 with F.-B.0. Not one single individual in the categories F.-B.3, 2 or 1 had the slightest trace of food in its mid or hind gut. Hence feeding does not start until the fat-body is practically all used up (F.-B.0).

The distribution of the 335 females with F.-B.0, in relation to both the numbers of eggs contained and the amount of food material in the gut, is shown in Table VIII. Clearly, the average female in nature does not begin feeding until

TABLE VIII.

Gut condition in relation to number of full-sized eggs (A + B) in 335 females with F.-B.0 taken throughout Phase 1. (Gut: E = empty, F = containing a little food material, F+ = full, F++ = filled to distension.)

Numbers of eggs (A + B)	Numbers of individuals with gut condition				Percentage of individuals	
	E	F	F+	F++	begun feeding (F, F+, F++)	with gut well filled (F+, F++)
22–32	31	—	—	—	0·0	0·0
16–21	53	2	—	—	3·6	0·0
10–15	35	4	—	—	10·3	0·0
4–9	9	1	1	3	35·7	28·6
1–3	25	5	2	11	41·9	30·2
0	93	18	15	27	39·2	27·5

the major part of her eggs is laid. (This adds precision to the earlier conclusion, from laboratory experiments, that feeding starts "about the beginning of the oviposition period" (Milne & Laughlin, 1956).)

Decline of Fat-body during Phase 1.

As would be expected, the average fat-body content declines, and the percentage of F.-B.0 individuals increases as Phase 1 proceeds. This is illustrated in Table IX with the data for 1950 (other years showed the same). By the end of Phase 1, females on the sward have no fat-body remaining.

Approximately one quarter (27·3%) of individual females are still in fat-body category 3 at primary emergence (Table III). Therefore, when individuals with F.-B.3 no longer appear in random samples off the sward, the entire population must have completed primary emergence. None was found in the daily collections after 12th June 1950 (Table IX) nor after 19th June 1951. This confirms the field experiments on population emergence (Milne, 1959) which put the end of primary emergence at 11th June 1950 (97·6% of population), and at 19th June 1951 (100%).

TABLE IX.

Day by day details of fat-body remaining in females collected through Phase 1 of 1950. Females classified according to fat-body score.

Day of Phase 1	Total females in samples	Females with fat-body score 3	2	1	0	Mean fat-body score	Percentage individuals with F.–B.0.
2	1	—	1	—	—		
3	5	3	2	—	—	2·6	0·0
4	4	—	3	—	1	1·5	25·0
5	14	3	8	1	2	2·0	14·3
6	29	2	22	2	3	1·8	10·4
7	2 (Z)	—	—	1	1		
8	45	2	18	8	17	1·1	37·8
9	45	—	5	3	37	0·3	82·2
10	12	1	5	2	4	1·3	33·3
11 (12 June)	60	1	9	9	41	0·5	68·3
12	26	—	3	4	19	0·4	73·1
13	32	—	—	1	31	0·03	96·9
14	?(Z)						
15	—(Z)						
16	—(Z)						
17	—(Z)						
18	37	—	—	4	33	0·1	89·2
19	?						
20	8	—	—	—	8	0·0	100·0
21 (end)	?						

Sample size depended on the number of beetles active on any particular day. " Z " indicates days when, due to weather, there was little or, more usually, no activity; and " ? " indicates days when beetles were active but no observations were made.

Phase 2.

State on the Bracken.

The samples taken daily from the bracken throughout Phase 2 totalled 1,347 females for seasons 1949–1952. Of these, 259 individuals were collected at the height of the daily activity and 1,088 about one hour after activity was finished for the day.

Only 19 females had any fat-body remaining, and their percentages in the two groups were similar, *viz.*, 3/259 = 1·2 and 16/1088 = 1·5 per cent. Among these 19 the distribution of fat-body scores was 1 with F.-B.3, 8 with F.-B.2 and 10 with F.-B.1. The single individual with F.-B.3, taken after activity, was no doubt a primary emerger gone astray since it had an empty gut, an unswollen bursa copulatrix and, like individuals 1, 9 & 10 in Table III, eight full-sized eggs (A + B). Data for the remaining 18 individuals are shown in Table X. Females with fewer eggs than primary emergers having the same fat-body score may be presumed to have laid some of their eggs already. The means and ranges of numbers of eggs in Table X therefore suggest strongly that while some of the F.-B.2 could have been primary emergers or at least not yet begun ovipositing, others among the F.-B.2 and probably all the F.-B.1 individuals had already laid some of their eggs. Again, four of the eight F.-B.2 and eight of the ten F.-B.1 individuals had started to feed. These findings contradict the conclusions drawn from females taken from the grass sward during activity in Phase 1, namely, that oviposition does not start until the F.-B.0 stage (p. 472), nor feeding until the major part of the eggs is laid (p. 475). But the females providing the contradictory findings are less than 1·3 per cent. (*i.e.*, 18/1347) of all females active

over or resting on the bracken. Hence they may be regarded as aberrants. A possible reason for their aberrations will be given in a later paper.

By the time they come to the bracken, then, typical females (1328/1347 or 98·6%) have no fat-body remaining (F.-B.0). The next question is their egg content. Without doubt they have already laid eggs (see fig. 2 and Table XI).

TABLE X.

Details of 18 females in Phase 2 containing fat-body (F.-B.2 & F.-B.1), with a comparison of the mean and range of eggs in these 18 females and in primary emergers.

Fat-body score 2					Fat-body score 1				
	Total eggs					Total eggs			
Individual	A+B	A+B+C	Gut	Bursa	Individual	A+B	A+B+C	Gut	Bursa
1	7	8	F	?	9	0	4	F	?
2	9	11	F+	?	10	5	7	E	?
3	11	13	E	?	11	6	7	F+	?
4	11	14	F	L	12	8	9	F+	L
5	12	14	F	?	13	8	10	F++	?
6	13	15	E	?	14	9	10	F++	?
7*	13	15	E	?	15*	9	11	F	L
8*	15	19	E	S	16	10	10	E	?
	—	—	—	—	17	10	13	F++	?
	—	—	—	—	18	12	13	F++	M
Mean (and range) in above females	11·4 (7–15)	13·6 (8–19)	—	—	—	7·7 (0–12)	9·4 (4–13)	—	—
Mean (and range) in primary emergers	12·8 (8–21)	17·7 (14–25)	—	—	—	16·2 (11–26)	19·4 (12–27)	—	—

Gut symbols as in Table VIII; bursa copulatrix symbols as in Table VI; ? = no data. Individuals marked * from collections made at the height of the daily activity on bracken, others after activity finished; data for primary emergers from Table IV.

More than half have no A or B eggs left, nor will they produce any more full-sized eggs because that requires fat-body (adult feeding has no effect on production, Milne & Laughlin, 1956). Further, the mean over-all content, 1–2 eggs, is about the same as is normally present (unlaid) at death (see later). Hence it is obvious that typical females on the bracken have already completed oviposition. Of course, there will be exceptions, most likely among those with fairly large numbers of eggs still remaining.

Let us now compare females with F.-B.0 on bracken at the daily height of activity and an hour after activity has finished. Excluding females with no A and B eggs, then, during activity the mean content of A eggs was 3·80 (range 1–22) and of B eggs 2·39 (1–7); after activity the mean of A eggs was 3·80 (1–26) and of B eggs 2·34 (1–8). Obviously there is no difference here. But (see Table XI) after activity is finished, the proportion of individuals without any eggs (A or B) is somewhat higher than during activity, the difference being statistically significant. This was pursued further with respect to A eggs alone (because these

are ready to be laid) and with data for only those days in which both samples had been taken (often the samples alternated: a collection being made during activity on one day and after activity on the next). Among 162 females taken during activity and 214 after, the proportions without any eggs were, respectively, 61·7

TABLE XI.

Egg content of females in Phase 2 containing no fat-body (F.-B.0).

Collection	Number of individuals	A & B eggs combined			
		Per individual		Percentage individuals with	
		Mean	Range	0	0–8
(i)	172*	1·2	0–17	73·8	94·2
(ii)	256	2·0	0–22	51·2	94·5
(iii)	1,072	1·5	0–26	61·8	95·4

Collections made over four seasons, 1949–1952: (i) first day of Phase 2 or first night of roosting, *i.e.*, females coming to the bracken for the first time; (ii) throughout Phase 2 at the daily peak of activity; (iii) throughout Phase 2 about one hour after daily activity ends. Note: the increase in range of eggs per individual is to be expected with increase in sample size.

* This total is comprised of the appropriate individuals, *i.e.*, those from (ii) that were taken on first day of Phase 2, and those from (iii) that were taken on the first night of roosting, together with individuals from two areas neighbouring the study field.

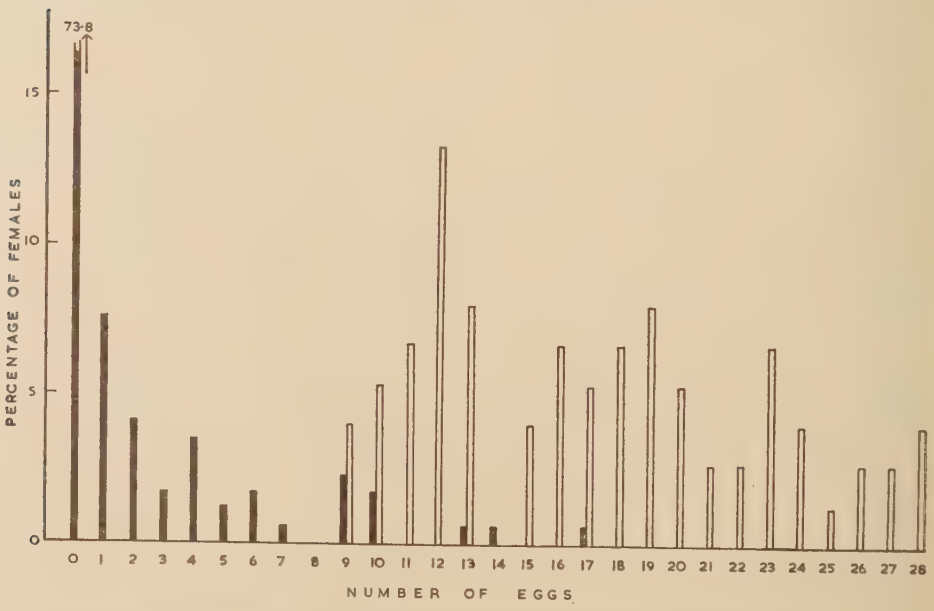


Fig. 2.—Egg content (A + B) of (1) females just before oviposition starts and of (2) females on their first visit to the bracken.

Data presented as percentage frequencies of individuals with respect to egg numbers: (1) White columns, derived from 75 individuals (see summarised data for F.-B.1 in Table V); (2) black columns, derived from 172 individuals (see Table XI, (i)).

per cent. (100 individuals) and 76·6 per cent. (164). The difference in proportion is statistically significant, χ^2 (and χ^2 corrected) being 9·797 (9·097) which with one degree of freedom gives $P<0·01$. From these facts it may be deduced that some individuals containing eggs leave the bracken between the height and close of daily activity; or, alternatively, that more such individuals leave than arrive. This is of interest in respect to ' bee-liners ' (see p. 481).

State on Hawthorn Hedge and Trees.

Circumstances on hawthorn hedge and trees are very much the same as on bracken, except for one minor difference, *viz.*, on hedge and trees no female with F.-B.3 was found but 5·6 per cent. (16 in 288) of individuals had some fat-body remaining (F.-B.2 and F.-B.1) as opposed to only 1·4 per cent. (19 in 1,347) on bracken. The difference in proportion, though small, is statistically significant ($\chi^2 = 17·52$, $P<0·001$). However, in Phase 2 on Upper High House Field, the portion of the population on bracken is very much larger than that on hedge and trees. Hence it may still be said that about 99 per cent. of phase-2 females are F.-B.0.

Gut Condition.

Feeding occurs outside the daily activity period—almost wholly in the early evening (Milne, 1958), and does not start until most of the eggs have been laid—which is after the F.-B.0 stage is reached (see p. 475).

Since very few beetles remain on the sward surface after activity (Milne, 1958), little feeding can take place on the grass sward. It is therefore not surprising that 73·4 per cent. of females with F.-B.0 taken from the grass during activity had the gut empty (Table XII). Indeed, it seems very likely that most

TABLE XII.

Proportions of F.-B.0 individuals in different gut categories on grass sward throughout Phase 1 during activity and on bracken throughout Phase 2 during and after activity. (For gut-content symbols see Table VIII.)

	Total females	Percentage individuals with gut E	F and F+	F++
Grass sward during activity ..	335	73·4	14·4	12·2
Bracken during activity ..	251*	6·0	22·7	71·3
Bracken after activity ..	1,064**	1·4	17·4	81·2

* No data for 5 of the 256 individuals.
** No data for 8 of the 1,072 individuals.

of the remaining 26·6 per cent. had not fed on the grass at all but on the bracken (or hedges or trees) the evening before. This is likely for two reasons: (1) the proportion of females spending the night on the sward surface is considerably less than 2 per cent. on the average—probably less than 1 per cent. (Milne, 1958, Table II; Milne, 1959, Table I); (2) F.-B.0 females *with food in the gut* never appeared in samples until *after* females first took to spending the night on the bracken (Table XIII).

Obviously, females start feeding after entering Phase 2. Of those taken from bracken during activity, 94 per cent. had food in the gut (Table XII). Since feeding does not occur during activity, typical females active on bracken must

have spent one or more nights thereon. For the same reason, one would expect more with the gut empty during than after activity. This is actually the case, for 6·0 per cent. of individuals during activity but only 1·4 per cent. after activity had the gut empty—a highly significant difference in proportion (χ^2, corrected = 17·01, giving $P<0·001$).

TABLE XIII.

Dates when females first appeared on grass sward in F.-B.0 state, first rested on bracken, and first appeared on grass sward in F.-B.0 state with food in the gut.

	First day that F.-B.0 females occurred on grass sward	First night that females rested on bracken	First day that any F.-B.0 females on the grass sward had food in the gut
Year			
1950	5 June	6–7 June	9 June
1951	15 June	15–16 June	22 June
1952	24 May	27–28 May	29 May

Observation of field behaviour suggested that the main feeding sites were the bracken, hedges and trees surrounding the grass sward, and this has been clearly confirmed by gut examination. The reason for this is, however, not at all clear. Since the beetle readily eats various sward constituents (preferring, for instance, salad burnet (*Poterium sanguisorba*) to bracken in the oviposition jar), migration to bracken, hedges and trees is not caused by the need for food.

Egg Content as Phase 2 progresses.

The picture here is the same whether samples are taken during or after activity. Samples after activity were larger and provide Table XIV. The

TABLE XIV.

Egg content of females on the bracken as Phase 2 progresses through its four quarters.

	Quarter of Phase 2			
	1st	2nd	3rd	4th
Individuals with no eggs	171	266	151	78
Individuals with eggs	60	168	130	48
Percentage individuals with no eggs ..	74·0	61·3	53·7	61·9
Mean egg content (and range) excluding individuals with no eggs	3·7 (1–17)	4·1 (1–22)	3·7 (1–26)	3·3 (1–11)

proportion of individuals containing no eggs does not vary significantly over the four quarters of Phase 2. Since the quarter is about five days long, this must mean that the average female lives only about $2\frac{1}{2}$ days after completing oviposition in nature. Otherwise, there would be an accumulation of spent females on the bracken, the percentage increasing from one quarter to the next. It is interesting

to recall that in the culture jar the average female lived for 2·4 days after laying her last egg (Milne & Laughlin, 1956). Naturally the range of egg content is greater the larger the sample, but both mean and range are significantly lower in the last quarter than in the preceding three quarters. In fact, during the final two or three days of the last quarter the range upper limit is usually in the region of four eggs. This shows that some females leave the bracken, because a significant drop in average content of females with eggs can only arise by subtraction (departure) of a sub-group with higher average content. The reason for the drop manifesting itself in the fourth quarter will emerge in a later paper of the series.

It will be noted that the individuals with some fat-body remaining (Table X) have been ignored here. They form such a small proportion of the bracken population that they make no difference to general egg content, but they are not unimportant in the question of ' bee-lining '.

Egg Content of ' Bee-liners '.

The ' bee-liners ' have been mentioned several times already. They are the females which shoot out suddenly from the mêlée of phase-2 activity on bracken or trees to alight upon the sward of their own or a more distant field. They will be dealt with fully in a later paper. Here only their egg content (A & B eggs) is considered.

Since they shoot off at high speed, bee-liners are extremely difficult to catch even when not flying out of reach of a long-handled net. It took three seasons to accumulate totals of 42 individuals bee-lining off bracken and 55 individuals off trees. Along with every sample of bee-liners, for comparison, a random sample of females was always taken at the same time off the bracken or trees from which the bee-liners issued. These random samples totalled 259 females from bracken and 82 from trees. They represent the ' parent population ', on bracken and trees, which ' produces ' the bee-liners (a minority, see later).

In the parent population on bracken, 1·1 per cent. of females (3/259) had some fat-body still remaining, and on trees 4·9 per cent. of females (4/82). Among bee-liners from the bracken, however, 14·3 per cent. (6/42) had fat-body remaining, and from the trees 10·9 per cent. (6/55). Combining the data, 2·1 per cent. of the parent population (*i.e.*, 7/341) and 12·4 per cent. of bee-liners (12/97) had some fat-body still remaining. This difference in proportion is highly significant ($\chi^2 = 16{\cdot}969$, $P<0{\cdot}01$). Clearly, individuals with some fat-body are more

TABLE XV.

Percentage distribution of individual females according to numbers of A + B eggs contained, (i) in the parent population on bracken and (ii) in bee-liners issuing from that parent population (F.-B.0 females only).

Eggs (A + B)	No. of individuals in each egg range		Percentage individuals in each egg range	
	(i) Parent population	(ii) Bee-liners	(i) Parent population	(ii) Bee-liners
0	131	4	51·1	11·1
1–5	96	9	37·5	25·0
6–10	21	8	8·2	22·2
11–15	4	7	1·6	19·5
16–20	2	4	0·8	11·1
21 & over	2	4	0·8	11·1

inclined to become bee-liners than those with none remaining, and the former generally have all their eggs yet to lay.

The vast majority (87·6%) of bee-liners, however, have no fat-body left. These F.-B.0 bee-liners issuing from bracken contained 9·47 eggs on the average though the parent population had an average of only 1·95 eggs. Similarly, bee-liners from trees contained 9·43 eggs as compared with 3·04 eggs in their parent population. Clearly the F.-B.0 individuals more inclined to bee-lining are those containing most eggs. For bracken, this point is illustrated in Table XV. The data for trees are similar.

In short, the bee-liners are mainly (almost 90%) individuals with eggs still to lay, and these may include an appreciable proportion (almost 12%) which have not begun to oviposit.

Reproductive State at Death.

Dead females are difficult to find in nature; many die where they cannot be seen, in the grass mat, bracken litter or soil; and the internal organs of most of those found are usually in an advanced state of decomposition. If the decomposition is not too far advanced, the number of residual mature eggs can be ascertained, but not the amount of fat-body remaining (if any). While slowly accumulating natural data, the question of reproductive state at death was examined frequently in laboratory experiments. Since these experiments all gave approximately the same picture, the results of one of the larger experiments will suffice for illustration.

In 140 experimental females only 17, or 12·1 per cent., had any fat-body remaining at death, that is, on the 0·05 probability, somewhere between 6·7 and 17·5 per cent. of individuals. Before dying, then, most experimental females have consumed the whole of their fat-body. The exceptions may have from 5 to 100 per cent. fat-body remaining, *i.e.*, die with anything between one and all of their eggs still not manufactured. Of the 17 individuals in this case, only one, with fat-body score F.-B.1, had laid any eggs. This confirms the previous conclusion

TABLE XVI.

Percentages laid of total mature eggs (A & B) produced in 140 females before death in breeding jars. Mean per female 75 per cent. (calculated on ungrouped data).

Percentage laid of eggs (A & B) produced	Numbers of females
0	20*
1– 9	5
10–19	2
20–29	0
30–39	1
40–49	2
50–59	3
60–69	3
70–79	2**
80–89	11
90–99	11
100	80

* 16 of these 20 females had some fat-body remaining (F.-B.1, 2 or 3) but none had laid any eggs.

** 1 of these 2 females had some fat-body remaining (F.-B.1) and had laid a few eggs.

All the other (123) females had no fat-body remaining (F.-B.0).

that it is unusual for oviposition to start before the fat-body has been all consumed in the manufacture of eggs.

In the 123 females with no fat-body left at death, the mean number of class-B eggs remaining was 0·03 (0–1), and of A eggs 1·72 (0–19). Thus most experimental females not only manufacture all the full-sized eggs possible from their stores laid down in the larval stage but also lay, on the average, all but about two of these eggs before death. Two eggs, however, is 12 per cent. of the total production of the average female (see p. 473). And when females failing to lay at all are included, only 75 per cent. of the actual egg production of an experimental population is actually laid, as is indicated in Table XVI. This is of course due to premature death, and any individual not laying all the eggs it produces may be considered to have died prematurely. On this ruling, rather less than half (60/140 or 43%) of the experimental population died prematurely. In nature, where there is no protection from predation, the percentage dying prematurely will, of course, be larger.

The total sample of dead beetles from nature amounted to 25 individuals. Their fat-body condition was uncertain. In Table XVII. the numbers of mature

TABLE XVII.

Residual mature eggs in females after death in nature and in laboratory experiment.

Residual eggs A + B	Numbers of females	
	In nature	In jar experiment
0	15	84
1	1	9
2	1	8
3	1	3
4	1	4
5	2	1
6	—	3
7	1	1
8	1	5
9	—	2
10	1	4
11	—	1
12	—	2
13	—	1
14	—	2
15	—	1
16	—	2
17	—	2
18	—	1
19	—	2
20	—	1
21	1	—
22	—	—
23	—	—
24	—	1
Total females	25	140

eggs (A and B) in the natural and experimental samples are compared. The agreement is quite close: the means of residual eggs were 2·6 and 3·1*, respectively, and in both cases about 60 per cent. of individuals had no mature eggs remaining at all.

* In four other experiments of 40 individuals each, the mean residual eggs ranged from 2·2–3·8.

Conclusions.

At various stages in the preceding text, individual behaviour has been logically deduced from mass aspects of female reproductive state throughout the two Phases. It is useful to bring all these deductions together now, in proper sequence.

Individual behaviour in Phase 1.

On the day of her primary emergence, the female copulates and returns into the sward—but not to oviposit. Instead, she repeats the emergence performance on one or more days until her full complement of eggs is matured, the fat-body being then entirely consumed. Only now does she begin oviposition. After laying all or most of her eggs (possibly punctuating the process with one or more reappearances above ground), she leaves the grass sward during the normal daily activity period and flies to the surrounding bracken (or hedges or trees). This is her entry into Phase 2.

Individual behaviour in Phase 2.

In the evening of her arrival on the bracken (or other fringing vegetation) she begins feeding for the first time (on the fronds, or leaves, etc., on which she rests). If finished ovipositing (as in most cases), she remains thenceforth on the bracken, taking part daily in the activities there until her death. If not finished with egg-laying, then next day or later she flies off (bee-lines) to finish the job (hence the females found in the latter part of Phase 1 with food in the gut); and, should she not die in the soil after completing oviposition, she returns to the nearest bracken, hedge or tree to end her days there.

There is a limit, of course, to what can safely be deduced from mass phenomena, and obviously the above description of individual behaviour requires confirming here and filling out there. This is done in a later paper by direct field observation and quasi-natural experiment on selected individuals.

A practical consideration.

When bushes or tree branches are shaken vigorously in the evening, all the chafers thereon will fall readily on a collecting sheet spread on the ground below. Traditionally, the gardener has been advised to ' control ' the garden chafer by collecting all the adults in this way and destroying them. But clearly, from the present investigation, mass oviposition has occurred in Phase 1, and females are practically spent before entering Phase 2, *i.e.*, before taking to the bushes or trees. Hence, if the chafers came from the gardener's own land they would have already laid practically all their eggs there, and for him to follow the traditional advice would be utterly futile. Even if his land were as yet uninfested, it is doubtful if destruction of adults on his own bushes and trees would be worth the effort. There would usually still be far more potential colonisers, as bee-liners, in a wide area surrounding his garden.

Summary.

This part of the study of the garden chafer, *Phyllopertha horticola* (L.), in the English Lake District deals with the reproductive state of the females during the flight season. Total egg-production depends entirely on stores (fat-body) accumulated in the final larval instar. On the average, the fat-body enables about 16 or 17 mature eggs to be manufactured per female, the usual range being 9–32. Rate of reproductive development is the same in the largest and smallest female adults. The outstanding mass features of the flight season are the two roughly equal and half-overlapping Phases: Phase 1, swarming over the grass sward, followed by Phase 2, swarming on the surrounding bracken, hedges and trees. Mass aspects of the female reproductive state throughout the two Phases are as follows.

At primary emergence on the grass sward, females always contain some fat-body together with some fully developed and/or immature eggs. On the average they have about one-third of their full complement of eggs matured, the range being from none (with about 50% of the original fat-body still remaining) up to four-fifths (with about 10% of the fat-body). Since primary emergences in a homogeneous population extend over about a fortnight, females taken from the grass sward throughout Phase 1 are in various reproductive states. Thus after the first few days of the Phase and until the last individual makes its primary emergence, sample females may have half their fat-body and no eggs yet fully matured or no fat-body and all their eggs actually laid, or any intergrade between these extreme states. Towards the end of Phase 1 (which finishes about a week after the last primary emergence), females have no fat-body remaining and have already laid most or all of their eggs; and a small proportion of them now has food in the gut.

In Phase 2, about 99 per cent. of females on bracken, hedges and trees contain no fat-body and therefore cannot manufacture any more eggs. On the average they have two mature or very nearly mature eggs left (range 0–26). This egg content is much the same as at death. The remaining 1 per cent. of females are aberrants with some fat-body still unconsumed. 'Bee-liners', the females which shoot out bullet-like from the bracken, hedges or trees to alight comparatively far afield, either have some fat-body remaining, or, if not, considerable numbers of eggs (mean about 9 as compared with the general mean of 2). Thus bee-liners are the phase-2 individuals with most eggs still unlaid. Obviously they are a minority.

Deductions as to individual behaviour are made from the mass aspects of the reproductive state and are to be examined in the next paper of this series.

Since females of the garden chafer have already laid all or most of their eggs before appearing on hedges and trees, gardeners will not control this pest by killing all they find on their hedges and trees.

Acknowledgements.

Thanks are due to Professor V. B. Wigglesworth, C.B.E., F.R.S., who, on a visit to our field station in the middle of the 1948 flight season, dissected several females which he found mating on the bracken; his remarks on the spent condition of these females, in effect, led me to the idea that a serial study of reproductive state in wild garden chafers might well be illuminating. Thanks are also due to Messrs. T. P. McNicol and R. Coggins for help in field collecting, and to Mr. R. Laughlin, M.A., for criticism of the manuscript.

References.

Laughlin, R. (1956). Storage and utilization of reserves by the garden chafer, *Phyllopertha horticola* (L.).—*J. exp. Biol.* **33** pp. 566–575.

Milne, A. (1956). Biology and ecology of the garden chafer, *Phyllopertha horticola* (L.). II. The cycle from egg to adult in the field.—*Bull. ent. Res.* **47** pp. 23–42.

Milne, A. (1958). Biology and ecology of the garden chafer, *Phyllopertha horticola* (L.). IV. The flight season: introduction, and general aspects.—*Bull. ent. Res.* **49** pp. 685–699.

Milne, A. (1959). Biology and ecology of the garden chafer, *Phyllopertha horticola* (L.). V. The flight season: sex proportions.—*Bull. ent. Res.* **50** pp. 39–52.

MILNE, A. & LAUGHLIN, R. (1956). Biology and ecology of the garden chafer, *Phyllopertha horticola* (L.). I. The adult and egg production.—*Bull. ent. Res.* **47** pp. 7–22.

RAW, F. (1951). The ecology of the garden chafer, *Phyllopertha horticola* (L.) with preliminary observations on control measures.—*Bull. ent. Res.* **42** pp. 605–646.

RITTERSHAUS, K. (1927). Studien zur Morphologie und Biologie von *Phyllopertha horticola* L. und *Anomala aenea* Geer (Coleopt.).—*Z. Morph. Ökol. Tiere* **8** pp. 271–408.

© Commonwealth Agricultural Bureaux, 1959.

INVESTIGATIONS ON *HELIOTHIS ARMIGERA* (HB.) IN UGANDA.

By T. H. Coaker *

Empire Cotton Growing Corporation, Cotton Research Station, Namulonge, Uganda.

Heliothis armigera (Hb.) is a well known pest of many economic crops in Africa, and in East Africa it is generally regarded as a serious pest of cotton. However, its status varies from that of relative unimportance in Uganda to that of a limiting factor to cotton production in some parts of Tanganyika (McKinlay, 1956, 1957).

Parsons (1939, 1940*a*, *b*), Parsons & Ullyett (1934) and Jones (1936, 1937) made intensive studies of the bionomics of this pest in southern Africa under conditions of high annual populations. The investigations described in the present paper were carried out under conditions of low population densities. They included a survey of the pest on crops grown under an intensive farming system at the Cotton Research Station; although unlike the general agricultural conditions found over the greater part of Uganda, the station offered a suitable environment wherein the annual course of *Heliothis* activity could be studied. Various biological observations were also made, with particular emphasis on determining why the population remained low under the local conditions.

Climatic and Agricultural Conditions.

The Cotton Research Station, Namulonge, is situated in the province of Buganda, approximately 30 miles north of the equator. It is generally representative of the southern cotton zone of Uganda and it is reasonable to suppose that, even with the slight climatic and ecological differences that occur over this area, the general behaviour pattern of *Heliothis* is similar over the greater part of it.

In this region there are two main rainfall peaks, one in the early rains (those falling between March and June) and the other in the late rains (those falling between September and November). In every month of the year a certain amount

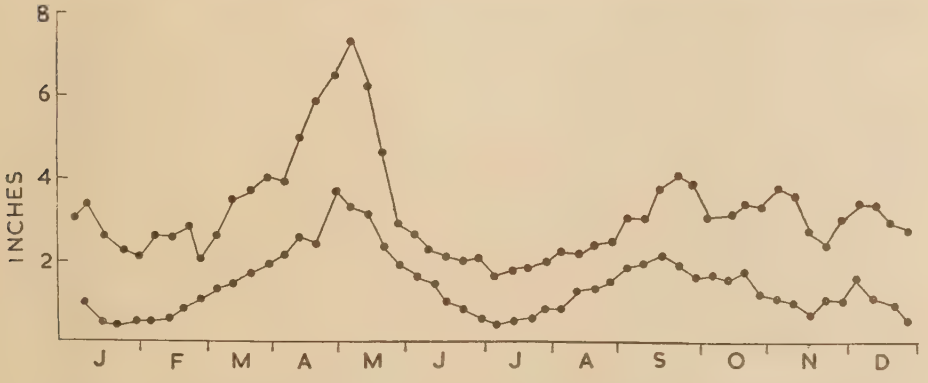


Fig. 1.—1:1 confidence limits of three-weeks moving totals of rainfall, in inches, at Namulonge, Uganda. Data for 10 years (1947–56). Adapted from Manning (1956).

* Now at National Vegetable Research Station, Wellesbourne, Warwicks.

of rainfall is expected, as is shown in fig. 1. The two curves represent the 1:1 confidence limits of the three-weeks moving totals of rainfall, calculated from the records taken at Namulonge over the 10-year period, 1947–56. This method of expressing rainfall expectation was developed by Manning (1956) and the lower curve, representing the lower limit of rainfall expectation, shows clearly that some rainfall is to be expected in every month of the year. This is an important point, since, taken together with the small range in annual temperature (Table I), it

TABLE I.

Mean monthly temperatures (°F.) recorded at Cotton Research Station, Namulonge, Uganda.

	1954		*1955*		*1956*		*1957*	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
January ..	86·0	58·6	83·5	59·8	81·9	59·2	82·9	57·1
February ..	86·7	60·8	82·3	62·1	83·2	59·0	83·3	58·7
March	86·1	62·9	83·5	63·5	86·3	61·4	81·2	60·2
April	81·7	63·8	82·3	62·7	81·2	61·9	80·2	61·0
May	81·1	62·6	81·4	63·1	80·4	61·4	80·4	61·0
June	80·7	61·5	81·5	60·2	80·0	59·4	80·6	58·6
July	79·4	59·9	81·2	59·9	80·7	56·2	81·3	57·1
August	79·4	60·2	83·3	60·8	81·3	58·8	80·3	57·9
September ..	80·9	60·2	80·9	60·5	80·5	59·4	85·3	57·1
October	80·0	60·3	83·1	60·3	82·0	59·6	84·8	59·8
November ..	86·6	61·4	83·8	60·6	83·1	59·5	83·4	59·4
December ..	81·6	61·4	82·6	60·3	82·0	58·7	81·2	58·8

means that conditions are favourable for plant growth throughout the year. Alternative wild host-plants of *Heliothis* are therefore quite common and, together with abundant cultivated host-plants, constitute a continuous succession throughout the year.

At Namulonge, a farming system has been developed, whereby two successive arable crops are grown each year on the same land, thereby utilising the bimodal pattern of rainfall to its fullest extent. The farming system is, briefly, as follows: in the first year of cultivation, maize (*Zea mays*, variety K8) is sown in late February and is usually harvested in June. The following cotton crop (*Gossypium hirsutum*, variety BP52) is sown immediately after the maize has been harvested and is ready for picking in the early part of the following year. In the second year, groundnuts (*Arachis hypogaca*) are grown, followed by dwarf beans (*Phaseolus vulgaris*), and in the third year, maize followed by cotton completes the succession. Usually this succession of arable cropping is then followed by three years of grass fallow, but may in some cases be repeated as a further three-year cycle before the land is put down to grass.

The areas under cultivation at Namulonge are arranged as strips, approximately on the contour, and in many instances 30–50 acres of a given crop may be grown in contiguity. Such conditions contrast in the extreme with the holdings of the local African farmers, who rarely grow more than one or two acres of any one crop as a continuous area. This is, in turn, often surrounded by uncultivated bush separating it from the next area under cultivation. Similarly, the cropping routine has little or no regular sequence and all the crops mentioned in the Namulonge system may be found growing at any time, except cotton, which is always grown over the same period of the year.

A Survey of egg and larval Populations of *H. armigera* on cultivated Crops.

The main object of the survey was to determine the annual cycle of activity of *H. armigera* under the intensive farming conditions at Namulonge. The rôle of *Heliothis* as a pest of cotton in Uganda has usually been considered a minor one (Taylor, T. H. C. *in* Tothill, 1940, p. 276), but with large contiguous areas of cultivated host-plants grown in almost continuous succession, conditions seemed likely to favour the survival of large populations. Michelmore (1955, 1956) thought that *Heliothis* was becoming more abundant with the increase of maize grown in Uganda. Information on the incidence of *Heliothis* gathered over a series of years should reveal the effect of the cropping system on the carryover from one crop to another, and offer interesting comparisons with the areas in Africa where attack by *Heliothis* causes severe losses to various crops.

The main emphasis in the survey was placed on the maize-cotton sequence of the rotation system. The numbers of eggs and larvae found on groundnuts and beans were low, and the records obtained have to a certain extent been omitted, as they had apparently little relevance to the ultimate populations found on cotton.

In one year, maize was grown for experimental purposes, as a continuous succession of sowings alongside an adjacent cotton crop, so that the flowering cycles of the two crops coincided. Parsons (1939) found that under South African conditions, with a high *Heliothis* density, maize was a more attractive host than cotton and therefore acted as a trap crop. Sunflower was also tried under similar conditions of sowing and proximity to a cotton crop, following observations at Namulonge indicating that it, too, was a favoured host-plant.

Sampling method.

The sampling method used to determine the distribution and abundance of *H. armigera* eggs on maize was similar to that developed by Marshall (1936) in South Africa. Although this method was developed on much denser populations than those in Uganda, the results obtained were considered sufficiently reliable to give comparative records of *Heliothis* activity on the various crops examined.

An area measuring 200 yd. by 34 yd. was taken from the centre of a larger area of the crop to be sampled. At Namulonge, all the crops are grown on strips 34 yd. wide, with one yard between the rows. The length of these strips varies, but in the crops examined, all exceeded 200 yd.; the area sampled was chosen from the middle of a strip and extended completely across it, so that any possible edge effect was included in the sampling area. The sampling area was divided transversely into five equal portions, and four observation points were taken in each portion, totalling 20 over the whole sampling area. The points were so arranged that a lateral scatter was obtained; five rows separated each point, thus the series of points moved diagonally across the field. Ten of the 20 sampling points were taken in one direction along the sampling area, and ten were taken in the return direction. Each series of points was situated along diagonally opposite lines so that the whole area was likely to be covered by the random sampling. At each point one square yard of the field was sampled, or one running yard of row. Plants that were sampled for eggs were taken on the right-hand side of the sampling point (looking up the strip), those on the left-hand side being sampled for larvae. Since the minimum incubation period for eggs of *Heliothis* was four days, it was necessary to sample the same plants twice each week to obtain the true oviposition rate. The figures given for egg populations throughout this paper thus represent the numbers of eggs laid per week. Larvae were only sampled once each week and figures given in this paper represent the populations of larvae present on each occasion. Both the eggs and larvae found were removed from the plants and brought into the laboratory for further investigations. The sampling positions were moved weekly, to avoid any handling effect that might interfere

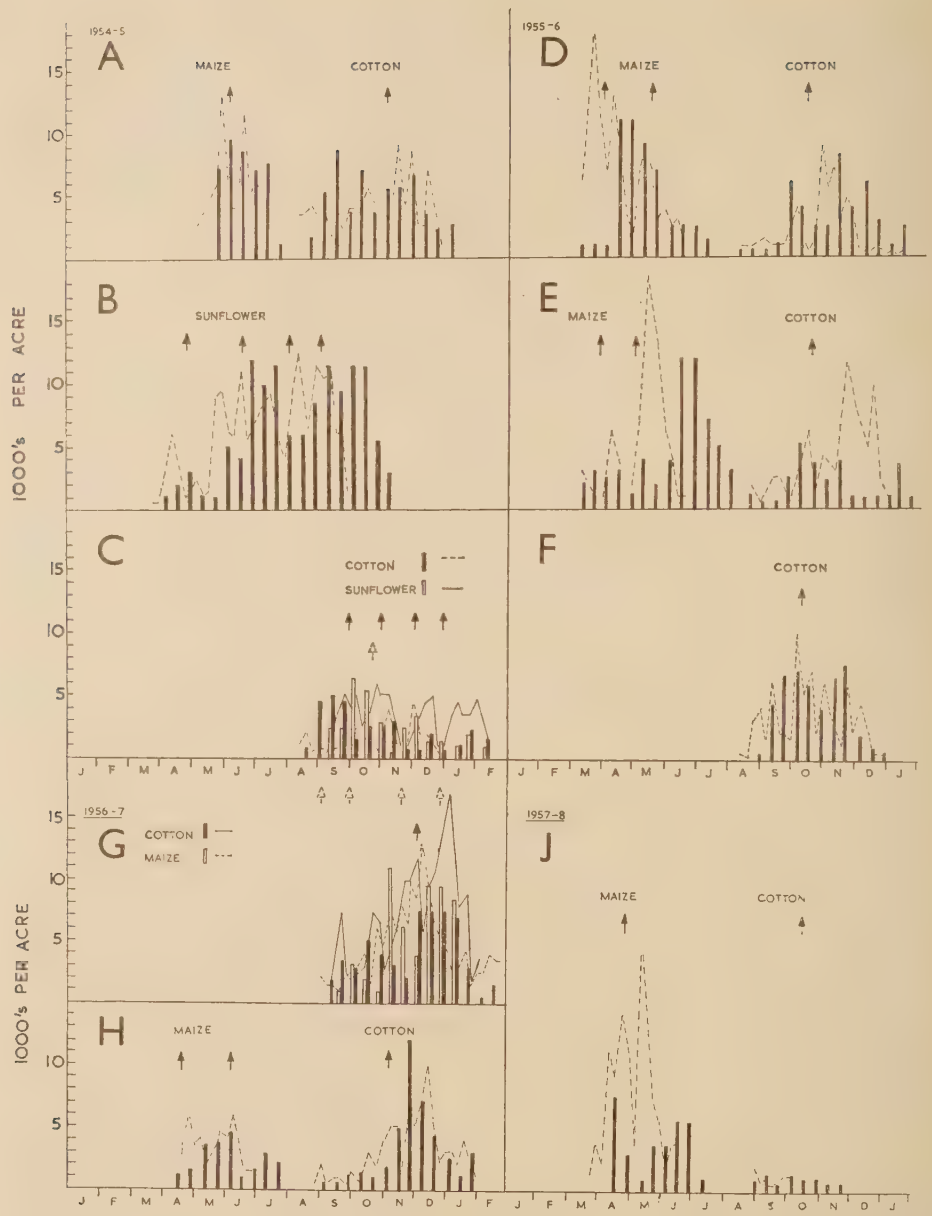


Fig. 2.—Populations of *Heliothis armigera* on cultivated crops at Namulonge, Uganda. Graphs represent numbers of eggs laid per week, histograms represent total larval populations present. Dates of peak flowering of host-crops indicated by arrows.

1954–55: A, maize followed by cotton; B, four successive sowings of sunflower; C, sunflower and cotton grown adjacent to one another.

1955–56: D, maize followed by cotton; E, same as D, but another locality; F, cotton not preceded by another crop.

1956–57: G, cotton and maize grown adjacent to each other; H, maize followed by cotton.

1957–58: J, maize followed by cotton.

with the plants' normal growth, and thereby affect their attractiveness to ovipositing moths; also, the progressive movement along the row increased the area sampled. So that only the true oviposition rate would be determined, all the eggs present on the plants at the sampling points to be used in any given week were removed three days before the first recorded observation was made.

All sampling commenced 2–3 weeks before flowering and continued until senescence, or until the numbers recorded were too low to make assessment reliable. The whole plant was searched for eggs and larvae. On cotton and other monoclinous plants, the eggs and larvae were invariably found on the young tissues and fruiting bodies. On the maize plant, which is diclinous, the eggs were mainly distributed on the silks (pistillate flowers) and over the upper two-thirds of the plant, as shown in Table II. The larvae were mainly confined to the cobs and tassels (male inflorescences).

TABLE II.

Oviposition sites of *H. armigera* on maize. Total observations over 4 seasons (1954–57).

	Top ⅓rd of stem*	Mid ⅓rd of stem*	Bottom ⅓rd of stem*	Top leaves	Mid leaves	Bottom leaves	Tassel	Silk	Husk
No. of eggs	156	122	2	113	56	3	72	284	75
% of total	17·7	13·8	0·2	12·7	6·3	0·3	8·2	32·2	8·5

* Includes the parts of the stem that are closely enfolded by the base of the leaf.

Although the survey was primarily conducted to observe *H. armigera*, larval counts were also made on the cotton crop of the other important Lepidoptera injurious to the cotton plant in Uganda, namely *Earias* spp.* and *Argyroploce leucotreta* Meyr.

Annual populations.

1954–55 (fig. 2, A–C).—During the first year, eggs and larvae of *Heliothis* were sampled on (a) the maize-cotton sequence, (b) a succession of sunflower sowings producing a continuous sequence of flowering between April and November, and (c) on adjacent sunflower and cotton crops whose respective flowering cycles coincided. The last observation was made so as to test the relative attractiveness of the two crops to *Heliothis* oviposition.

Each series of observations was made on various parts of the farm and no two were so close together as to exert any considerable influence on their respective populations. In all cases, and in every year in which observations were made, the crops sampled were chosen from as widely separated areas as possible, in most cases from 2–3 miles apart. The maize crop preceding the cotton crop was sown in late March and became attractive to ovipositing moths by the beginning of May, approximately two weeks before the opening of the male inflorescences. The oviposition rate increased with flowering, so that peak flowering and peak oviposition were reached at approximately the same time. Larvae were first recorded in late May, reaching peak numbers one week after peak oviposition. The numbers recorded of both eggs and larvae dropped as the crop ripened. Estimated peak numbers on the maize crop were 13,000 eggs and 10,000 larvae per acre. On the following cotton crop, sown in June, oviposition commenced two weeks

* *Earias biplaga* Wlk., *E. insulana* (Boisd.) and the less well known *E. cupreoviridis* (Wlk.).

before the first flower opened, increased with the rise in the flowering rate and dropped sharply once the flowering rate fell off. Although the harvesting of the cotton crop was not completed until the end of February, sampling for eggs and larvae was stopped in January, as at that time few flowers were being produced, the majority of the bolls were fully developed and splitting, and too few eggs and larvae were being recorded to be accurately estimated.

The succession of sunflower sowings produced an attractive phase to *Heliothis* for eight months, but although the numbers recorded rose steadily to 11,000 eggs and larvae, respectively, per acre, when the second sowings were fully in flower, successive sowings did not harbour larger numbers. As in the case of maize, peak oviposition coincided broadly with peak flowering of each sowing in the succession.

The moths oviposited on the sunflower plant in close vicinity to the developing flower buds, namely on the surrounding leaves and bracteoles, starting when the bud first began to show. The larvae feed on the young florets or, more often, on the pithy receptacle. On some plants, up to 13 larvae were found on one head, positioned around it like figures on a clock face.

Good distribution of the larvae on the food-plant would possibly result in less cannibalism amongst them. On sunflower, where such a distribution was found, the egg/larva ratio was low compared with that in maize, suggesting a lower larval mortality in the former crop. The majority of the larvae found on the maize plant were feeding on the cob, and to gain access to it they entered the husk *via* the silks; at that time they would be especially likely to come into contact and this would favour their cannibalistic tendencies. Barber (1936) bred maize with long, tight husks and thus reduced the amount of damage caused by *Heliothis*, since the conditions favouring cannibalism were increased and the number of larvae reaching the cob was considerably reduced.

Where the cotton and sunflower crops were grown adjacent to each other, the numbers of eggs and larvae recorded were approximately half that recorded on the earlier sunflower succession or on the cotton crop following maize. The number of eggs at peak oviposition was between 5,000 and 6,000, recorded in late October at maximum flowering of the second planting. The numbers of larvae present were similar on the two crops. On the cotton crop neither eggs nor larvae exceeded a rate of 5,000 per acre and generally remained much lower. There are two possible reasons for the low numbers recorded on the two crops: (a) the population in the particular locality in which the crops were grown was low, or (b) the available population distributed itself equally over the two crops, each crop being of equal attractiveness to the ovipositing moths.

1955–56 (fig. 2, D–F).—Observations on sunflower could not be continued this year because this crop was not grown again on account of its uneconomical status; more attention was therefore given to the maize-cotton succession. The populations on two such successions were followed in widely separated parts of the farm. Observations were also made on cotton that was not preceded by any other attractive host-crop in its vicinity.

The cycle of *Heliothis* activity recorded on the maize-cotton succession resembled that of the previous year, but showed a slightly higher rate of eggs and larvae on maize at the peak periods, although the cotton did not harbour as great a larval population as did the cotton following maize in 1954–55. The populations on the cotton grown away from any other host-crop did not differ materially from those on cotton following maize. The number of *Heliothis* recorded on cotton would appear to have been little influenced by the proximity of the maize crop grown in the first half of the year.

1956–57 (fig. 2, G, H).—The main observation made was on the effect of a maize crop on the number of *Heliothis* recorded on an adjacent cotton crop. As with the sunflower-cotton experiment already described, a succession of maize sowings was made so that flowering would be continuous and would coincide with

that of the cotton crop. As a comparison with the numbers of *Heliothis* recorded on this experiment, and to determine the relative attractiveness of each host-crop, the population on a normal maize-cotton succession in another part of the farm was also observed. The oviposition rate recorded on the maize succession increased with the later sowings to an estimated peak of 17,000 eggs per acre at the end of December. Numbers of larvae, however, remained much lower. On the adjacent cotton crop, the populations were similar to those in previous years and to that of the same year in a different part of the farm away from the influence of another host-crop. The population on the first-rains maize crop was low compared with that of the previous year on first-rains maize and with that of the maize succession grown later in the year. The relative attractiveness of the two crops, maize and cotton, appeared to be similar, with no apparent reduction in the numbers of *Heliothis* on cotton due to a preference for maize on the part of the egg-laying moth such as was reported from South Africa (Parsons, 1940*a*).

1957–58 (fig. 2, J).—The only observations made during this period were on one maize-cotton sequence. Although the oviposition rate on maize was high, numbers of larvae were low in proportion. On the cotton crop, the numbers of eggs and larvae were lower than had previously been encountered, which made the recording of them too inaccurate to warrant further observation. A possible explanation of the small number of larvae on maize and the extraordinarily few eggs and larvae on the following cotton crop was that during April and May unusually high rainfall was experienced, which may have reduced the proportion of larvae surviving on maize, and thus the density of moths later in the year, reflected in the low oviposition rate on the cotton crop. Many larvae died as a result of a nuclear polyhedral virus disease (Coaker, 1958) over this period, as compared with other years, suggesting that the conditions prevailing in April and May favoured an epizootic.

Observations on groundnuts and beans.

Observations were made on groundnuts, grown on the early rains, over the three years, 1955–57 inclusive. Oviposition was concentrated on the young foliage surrounding the inflorescences, and the larvae were usually found feeding on the very young leaves.

During the 1955 and 1956 seasons, the populations encountered were similar, with peak numbers of eggs of between 13,000 and 14,000 per acre, recorded at the end of May, at the latter end of the flowering cycle, approximately a month before the foliage became senescent. Larval numbers were low in proportion to the number of eggs recorded, reaching a peak of only 5,000 per acre, in mid-May.

In the 1957 season, egg-laying reached a peak of only 5,000 eggs per acre and larval numbers were too low for reliable estimation. As in the case of the maize crop of this year, the exceptionally heavy rainfall during April and May probably restricted the survival of the larvae.

The numbers of both eggs and larvae recorded on the crops of dwarf beans (*Phascolus vulgaris*) were never sufficiently high to make an estimation of the population reliable.

From these results it can be seen that the density of *Heliothis* on the crops examined is low in comparison with that encountered in other cotton areas of Africa, reported by Parsons (1939) and Valentine (1955), but that the annual activity is continuous, with no marked seasonal variation. On the maize-cotton succession, more eggs and larvae were recorded than on the groundnut-beans succession, with beans harbouring very low numbers. Oviposition cycles closely followed the crop flowering cycle. The yearly variation of populations was apparently no greater than the normal locality variation, and, despite ten years of increasing acreage brought under cultivation in the crops examined, there is no

indication that *Heliothis* is building up within the localised environment of a continuous host-plant succession.

Populations of *Earias* spp. and *Argyroploce leucotreta* Meyr.

Populations of larvae of both *Earias* and *Argyroploce* on cotton were estimated at the same time as those of *Heliothis*. The numbers of *Argyroploce* were very small, constituting two per cent. of the total population of the three genera on cotton. *Earias* spp. constituted 25 per cent., reaching a maximum of 5,000 larvae per acre in January 1955. During the preceding years, the peak numbers recorded varied between 2,000 and 4,000 per acre, and occurred at the end of the season, when most of the fruiting bodies held were green bolls. There was no relation between the population build up and the flowering cycle of the crop, as there was with *Heliothis*.

Earlier workers considered both *Earias* and *Argyroploce* to be more serious pests of cotton than *Heliothis*, and certainly more abundant (see Tothill (1940), pp. 268-275). They were, however, considering the country as a whole; in areas where maize is less abundant, possibly *H. armigera* also is less common.

Relationship of larval Numbers to Damage on Cotton.

The results of detailed assessments of crop loss have been reported by McKinlay & Geering (1957) and Coaker (1957), indicating that, under the conditions at Namulonge, losses due to insect pests in the latter part of the season affected the final yield more than damage caused at any other time of the season. The development of the larval populations of *H. armigera* and *Earias* was such that the maximum density was invariably recorded in the latter half of the season and it is possible that most of the damage then inflicted was caused by them.

The correlations of larval populations with damage to the fruiting bodies caused by Lepidopterous larvae (Pearson, 1950) are given in Table III.

TABLE III.

Correlation (expressed as R^2) of larval populations (expressed as numbers of larvae recorded per fortnight) with damaged fruiting bodies (expressed as numbers of buds or bolls showing damage caused by Lepidopterous larvae and collected in the same fortnight). Data from all 4 seasons included.

	Heliothis	*Earias*	Total larvae
Buds damaged	0·9498***	N.S.	0·8245*
Bolls damaged	0·6191**	0·4615*	0·6292*
Locules damaged ..	0·4067**	N.S.	N.S.
Yield per acre	N.S.	N.S.	N.S.

Levels of significance * $P = 0{\cdot}05$
** $P = 0{\cdot}01$
*** $P = 0{\cdot}001$

The highly significant correlation between numbers of *Heliothis* larvae and damaged buds reflects this species' habit of feeding more extensively on this type of fruiting structure than on any other; by contrast, larval populations of *Earias* are significantly related only to damaged bolls. The absence of any significant correlation with final yield was probably due to the large variation in yields between

localities and seasons. In view of this variation, presumably determined by some other environmental factor, such as water availability (Hutchinson, Manning & Farbrother, 1958) it can be concluded that *H. armigera* and *Earias* are not important factors in determining cotton yields in the Namulonge area.

Laboratory Breeding of *H. armigera*.

At the Cotton Research Station, a supply of all stages of *H. armigera* was required for experimental studies; it was important, therefore, to develop a simple technique for breeding in the laboratory. A method was devised to overcome the cannibalistic tendencies of the larvae (Barber, 1936), and to maintain the culture under fairly natural conditions, particularly as regards the pupal stage. It was carried out in a well ventilated insectary, as follows. The newly emerged moths were placed in a wooden framed cage measuring 3 ft. × 1½ ft. × 1½ ft. with a flat perspex roof and paper sides (originally the cage had wire-mesh walls, but these were found to attract the moths to oviposition). The moths were fed on a concentrated sucrose solution contained in 3 in. × ½ in. glass specimen tubes having a small piece of filter paper projecting from the top, as a wick. The sugar solution was changed every two days, otherwise mould growth, which was very rapid, soon covered the wick and surface of the solution. Cotton leaves standing in containers filled with water were put into the cages as oviposition sites. Almost without exception, the eggs were deposited on the leaves; various other surfaces were tested as oviposition sites but none was found to be as suitable as cotton leaves. The leaves bearing the eggs were put into a petri dish lined with moist filter paper and incubated at 24°C.; they hatched in approximately four days. On hatching, the young larvae were transferred into 3 in. × 1 in. glass specimen tubes containing portions of the food-plant. The tubes were plugged with cotton-wool wrapped in calico. If excessive condensation developed on the sides of the tubes, an open ended tube blocked at one end by a plaster-of-paris plug and at the other by cotton-wool could be used as an alternative. The plaster plug absorbed a considerable amount of the water vapour and little condensation resulted. Condensation should be avoided with the smaller larvae, as they often become trapped in the water and die. If the newly hatched larvae, that is, those up to two days old, could not be transferred to individual tubes after hatching, they survived satisfactorily on the cotton leaves contained in the petri dishes. The specimen tubes and food were changed every two to three days, depending

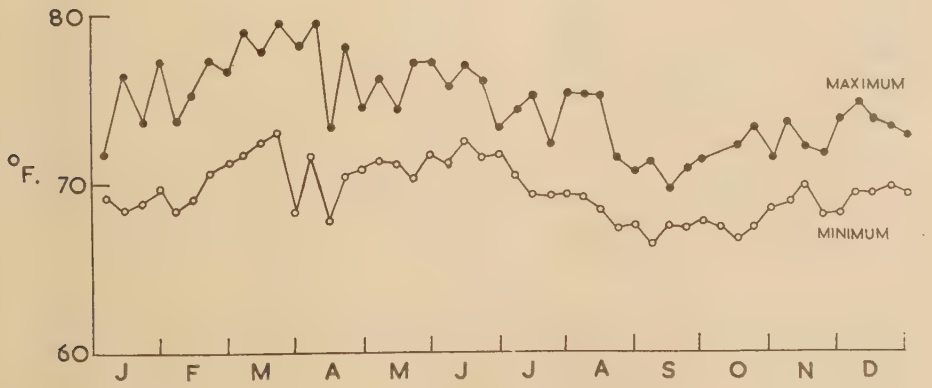


Fig. 3.—Maximum and minimum soil temperatures at 4-in. depth in pupation troughs. Namulonge, Uganda, 1955.

on the size of the larvae. Each fresh tube was previously sterilised to minimise bacterial and virus infections. When the virus infection began to limit the production of larvae, the eggs were dipped for 5 minutes into dilute (5%) Teepol and afterwards washed in distilled water.

When the larvae reached the prepupal stage they were transferred to pupate into cylindrical, perforated-zinc cages 6 in. long × 2 in. diam., previously filled with and sunk into soil in a concrete trough so as to leave about one inch exposed. Each cage was covered with a lid made of the same material, and thus retained the moth when it came to the soil surface after eclosion.

The concrete pupation trough was similar to that used by Parsons & Ullyett (1934) in South Africa for studies of *H. armigera* and *Diparopsis castanea* Hmps. It comprised a central trough (6 ft. × 3 ft. × 1 ft.) filled with soil and surrounded by a 4-inch-wide, water-filled, ant-proof trough. The trough was sheltered by a movable screen 2 ft. above the soil surface, so that the soil temperatures at 4-in. depth (fig. 3) could be adjusted to those obtaining at the same depth under field conditions.

This breeding method proved fairly satisfactory, but considerable work was involved in maintaining large numbers of larvae, as a mortality rate of between 40 and 50 per cent. was frequently experienced in the earlier instars.

The food fed to the larvae consisted of either 'milky' grains of sorghum, portions of the receptacle and corolla of sunflower, or flower buds of cotton. Sunflower was found to be most convenient, as it could be more readily grown throughout the year than the other food-plants.

TABLE IV.

Mean duration of larval and pupal periods of *Heliothis armigera*, in days.

Month	No. of larvae	Larval period		No. of pupae	Pupal period	
		Mean	Range		Mean	Range
January ..	28	20·0	19–23	11	20·2	16–25
February ..	43	21·3	17–29	36	19·9	14–21
March ..	77	21·2	16–26	52	20·6	11–33
April ..	46	18·3	14–23	30	20·5	15–28
May ..	36	32·1	24–42	17	22·7	21–25
June ..	19	24·0	16–28	7	21·1	19–24
July ..	21	24·8	14–31	8	20·4	17–24
August ..	86	21·9	17–33	69	22·6	16–38
September	47	26·5	22–33	34	27·7	23–33
October ..	59	25·1	22–32	33	26·0	23–43
November ..	33	26·0	25–28	16	26·3	24–28
December ..	37	27·1	22–34	24	26·1	22–31

Data from a culture reared on sorghum grains in an insectary, 1955. Air temperatures were similar to those shown in Table I and the soil temperatures recorded in the pupation trough are shown in fig. 3.

The average larval period over the year for over 500 larvae reared on sorghum grains was 24·8 days and the average pupal period for over 300 pupae was 22·9 days. The mean monthly values for the larval and pupal periods are given in Table IV. In neither case was there any pronounced seasonal variation or indication of diapause, and only occasionally did the pupal period exceed 30 days.

The frequency distribution of the pupal periods for the whole of the material is shown in fig. 4.

The preoviposition period of the female moth was 3·1 days (range 2–6), the oviposition period 10·4 days (range 8–12) and the fecundity rate 751·6 eggs (range 313–2,107); fertility was high, the percentage of eggs hatching being 71·4 (range 10–85·7). The peak oviposition period was between the third and sixth day after initial oviposition.

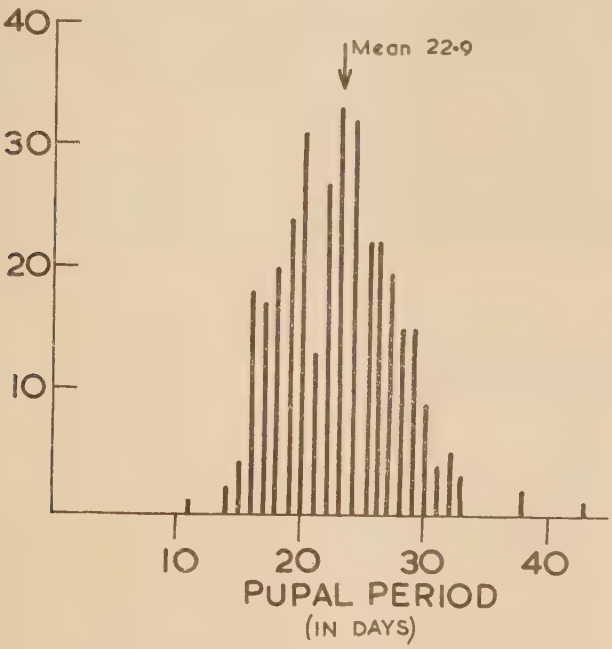


Fig. 4.—Frequency distribution of pupal periods (in days) of *Heliothis armigera*. Pupae in soil in open; larvae reared on developing sorghum grains in the laboratory.

Feeding Experiments.

The effect of different food-plants on the development of the larvae and pupae of *Heliothis* was studied in the laboratory. The diets were chosen from the various crops grown at Namulonge that were favourable to *Heliothis*. Newly hatched larvae were taken from the laboratory culture, reared on 'milky' sorghum grains, and put individually into sterilised 3 in. × 1 in. glass tubes containing a portion of the food-plant. The tubes and food were changed every 2–3 days. The larvae pupated in the tubes and the larval and pupal periods were recorded.

The various species and parts of plants fed to the larvae were as follows:

(1) Maize (*Zea mays*).
   (a) Silks (pistillate flowers).
   (b) Grains on the cob, aged 1, 3 and 5 weeks.
   (c) Mixed diet of varying cob age, corresponding to age of larvae, that is, one-week-old cob fed to first-instar larva, etc. Cob age was determined from the time the silks began to emerge from the sheath; after approximately five weeks the grains had reached full size but were not quite hard. Treatment (c) was chosen because the normal habit of the larva is to feed initially on the silks and thence gradually work

its way towards the cob. Treatment (c) therefore assumed nearly natural conditions, with the development of the larvae corresponding with the ageing of the cob. On the one-week-old grains the pistil was left intact.

(2) Cotton (*Gossypium hirsutum*).

(a) Flower buds (of such an age that the corolla was just exposed).

(b) Bolls aged 1, 3, 5 and 7 weeks from flowering.

The larvae do not naturally restrict themselves to feeding on one type or age of fruiting body, but move readily over the plant taking small amounts from buds and bolls in all stages of development. In the experiment, however, bolls were restricted to defined ages. Rainey (1948) showed that the developing ovules were richest in reducing sugars during the first three weeks of boll development and that thereafter the percentage dropped rapidly; similarly, the moisture content decreased from nearly 90 per cent. at the second week to under 65 per cent. at the eighth week; boll splitting was at 10 weeks. Younger bolls are preferred to older ones, but are not always available.

Difficulty was experienced in getting the smaller larvae to feed on the older bolls, but if a small portion of the carpel was removed, entry of the larva was facilitated.

(3) Sunflower (*Helianthus annuus*).

Portions of the flowering heads were used so that both corolla and receptacle were included.

(4) Dwarf bean (*Phascolus vulgaris*).

Young beans were used, collected soon after the corolla had been shed.

TABLE V.

Larval and pupal periods of *H. armigera* following feeding on different diets.

Treatment	Mean developmental periods (in days)	
	Larva	Pupa
Cotton flower buds	25·9 (3)	22·6 (6)
Cotton bolls : 1 wk. old ..	23·4 (9)	23·5 (4)
3 wk. old ..	22·7 (10)	23·6 (3)
5 wk. old ..	24·9 (4)	24·9 (2)
7 wk. old ..	31·1 (2)	26·0 (1)
Maize cob : 1 wk. old ..	22·2 (11)	21·7 (10)
3 wk. old ..	24·6 (5)	19·7 (12)
5 wk. old ..	23·6 (7)	20·6 (11)
Mixed ages ..	23·6 (8)	22·1 (9)
Maize silks	21·8 (12)	22·5 (7)
Beans	24·5 (6)	22·4 (8)
Sunflower	33·6 (1)	22·7 (5)
L.S.D. (P=0·05)	2·05	1·6
(P=0·01)	2·69	2·1
(P=0·001)	3·43	2·7

Numbers in parenthesis indicate positions of treatments in descending order from longest (1) to shortest (12).

Results.

The duration of the larval and pupal periods of material reared on the different diets is shown in Table V.

Since there was no possibility of lack of food affecting the length of the phases of the life-history observed, any deviation from the normal larval or pupal period was probably due to the effect on development of the food consumed. Most treatments had little such effect. However, of the cotton-boll diets, the older bolls tended to prolong the larval period, which was nine days more on 7-week-old bolls than on one-week-old bolls. Larvae fed on sunflower receptacle and corolla also had a longer period of development. Pupal periods were less affected, but tended to be slightly longer in those derived from larvae fed on older bolls.

Pupal Period.

The duration of the pupal period in material bred in the insectary and caged in soil outside (Table IV) or bred in the laboratory on various foods and allowed to pupate in tubes there (Table V), indicate no appreciable influence of season or of larval food.

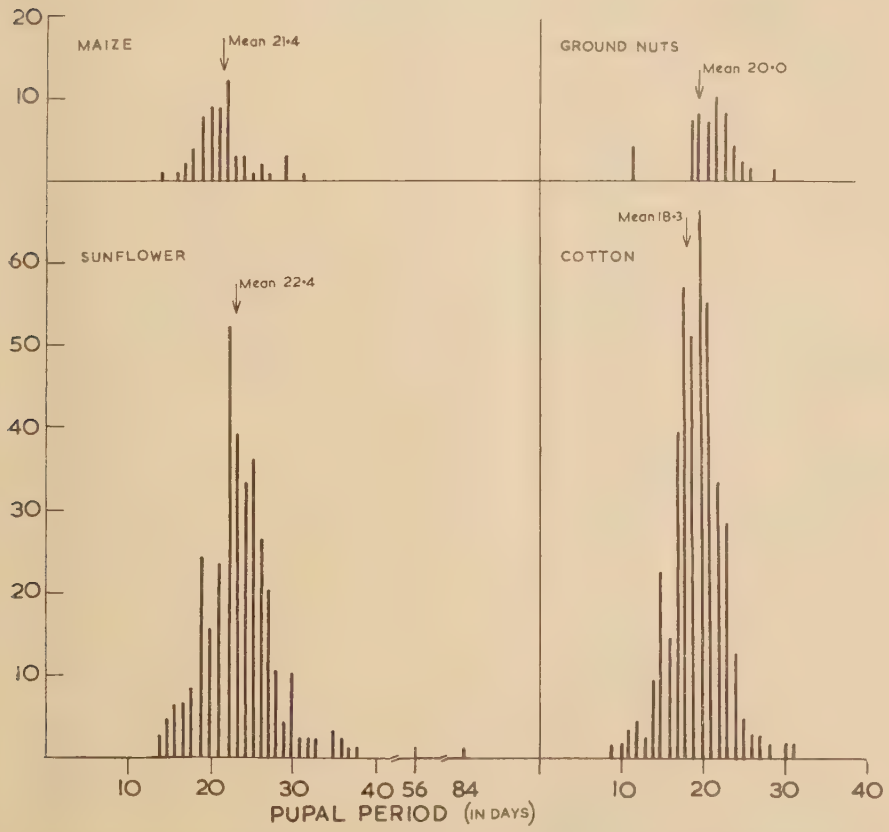


Fig. 5.—Frequency distribution of pupal periods from four successive seasons following larval feeding on various cultivated host-crops.

Further observations were made on larvae collected from the field during the population survey and brought to the laboratory and reared there by the technique described above. The larvae were fed on portions of food-plants similar to those from which they had been collected, namely, cotton buds, maize cob (up to two weeks old), sunflower corolla and receptacle, and young groundnut foliage. The frequency distribution of the pupal periods, collected over all four seasons, is given in fig. 5. These show little difference between the specimens collected on the various host-plants, mean pupal periods ranging between 18 and 22 days. Only in two pupae collected and reared on sunflower were long periods encountered (53 and 84 days).

The frequency distribution of the pupal periods of *Heliothis* collected and bred on cotton is shown for four successive seasons in fig. 6. All specimens were treated as described above, the larvae being reared inside the laboratory and the pupae outside of it.

It is concluded that no seasonal or annual resting or diapause stage is common amongst the population of *Heliothis* at Namulonge. It is interesting to draw

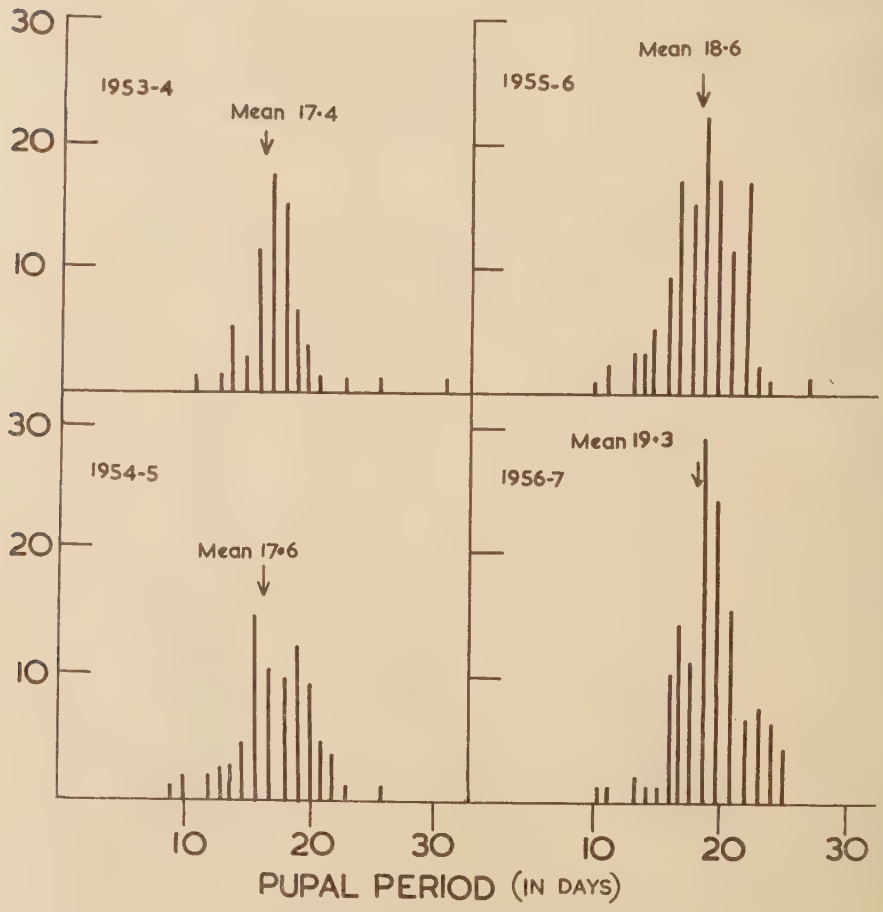


Fig. 6.—Frequency distribution of pupal periods from four successive seasons following feeding on cotton buds.

comparisons with observations made by other workers in Africa. Valentine (1956) demonstrated an increase in pupal period in July in Tanganyika; Parsons (1939) showed an earlier onset of diapause, a high proportion of the pupae formed in April and May not giving rise to moths until the following August–October. In both cases the longer pupal periods were recorded in the dry season, at a time when minimum temperatures are low compared with the rest of the year.

Diapause in *H. armigera* only occurs in a proportion of individuals in some generations, and is termed a " weak " facultive diapause by Andrewartha & Birch (1954, p. 58). Ditman, Weiland & Guill (1940) showed that diapause was induced in some of the pupae derived from larvae reared at 18·9°C., but that diapause did not occur in individuals reared at or above 24·4°C. The low temperature had its greatest influence if applied when the larvae were actively feeding, before the pre-pupal stage; once pupation had occurred, temperature had no further influence on diapause inception. In Uganda the seasonal temperature variation is small (Table I) and does not induce diapause. Further investigations are being carried out into the stimuli inducing diapause in *H. armigera*.

Parasites recorded from *H. armigera* **at Namulonge, Uganda.**

The following parasites emerged from the eggs or larvae of *H. armigera* collected from the field during the population survey on cultivated crops. All such eggs and larvae were brought into the laboratory and bred through.

Parasite	*Stage of host attacked*
HYMENOPTERA	
Scelionidae	
Platytelenomus hylas Nixon	Larva
Perilampidae	
Perilampus sp. near *tristis* Mayr	Larva (possibly hyperparasite)
Ichneumonidae	
Charops sp.	Larva
Enicospilus sp. ? *communis* Szépl.	Larva
Pristomerus sp. near *fumipennis* (Wlkn.)	Larva
Netelia (= *Paniscus* auct.) sp. ? *capensis* (Hlmgr.)	Larva
Braconidae	
Cardiochiles trimaculatus (Cam.)	Larva
Meteorus laphygmarum Brues	Larva
Neochelonella curvimaculata (Cam.)	Larva
Ascogaster sp. ? *cava* Saeger	Larva
Apanteles sp. (*ultor* Reinh. group)	Egg
Ceraphronidae	
Ceraphron sp.	Larva
Eurytomidae	
Eurytoma sp.	Larva (secondary, through *Apanteles*)
Chalcididae	
Brachymeria sp.	Larva (secondary parasite)
Trichogrammatidae	
Trichogramma sp.	Egg
DIPTERA	
Tachinidae	
Linnaemyia longirostris (Macq.)	Larva
Linnaemyia agilis Curr.	Larva

The monthly rate of parasitism, expressed as a percentage of the total number of larvae collected from each crop in that month during the four years of observation, is shown in Table VI. The data, however, should not be considered as indicating accurately the degree of parasitism, since obvious errors are involved; the total number of larvae collected included all stadia and since the majority of parasitised larvae would probably be found amongst the later instars, the inclusion

of all stadia may give a lower indication of the true rate of parasitism. Conversely, the percentage was calculated on the number of larvae collected and ignored mortality during the subsequent breeding in the laboratory; assuming that some of the larvae that died were parasitised, an underestimate of percentage parasitism would result. The data suggest, however, a variation from month to month of percentage parasitism in the crops sampled, expressed as a mean of the yearly

TABLE VI.

Percentage parasitism of larvae of *Heliothis armigera* by all parasites in each month of the year on various cultivated host-crops at Namulonge, Uganda. Means of 4 years' data (1954–57).

Crop	J	F	M	A	M	J	Jy	A	S	O	N	D
Cotton	0	–	–	–	–	–	–	–	10·8	3·8	2·1	0·9
Maize	–	–	–	0	9·0	23·8	0	–	–	–	3·3	0
Sunflower ..	2·1	–	–	–	2·5	9·3	6·4	7·9	3·5	10·0	25·0	8·3
Groundnuts ..	–	–	–	17·3	22·8	43·3	0	–	–	–	–	–

observations, with the highest rate occurring at the peak density of the *Heliothis* population. The peak levels of parasitism were not high and this is to be expected if the activity of *Heliothis* is continuous throughout the year at a fairly constant level, since under such conditions the parasites would probably exhibit similar activity patterns. The possible dispersal of *Heliothis* into other host-plants, in the period between the attractive phases of the cultivated host-crops, may be the reason for the very low rate of parasitism that followed initial infestation of each cultivated host-crop. The parasite, however, soon became established and built up with the increase in *Heliothis* density. Under such conditions of continuous activity, the respective *Heliothis* and parasite populations probably exhibit a state of equilibrium resulting in the low populations of parasitoids encountered. Parsons & Ullyett (1934), working with populations of *Heliothis* in which the activity cycle was extremely variable, with a distinct resting stage of three months during the year, obtained consistently high rates of parasitism once the population was re-established on the developing host-crop. The mean annual cycle of four years' observations on the four parasites most commonly encountered (*Apanteles* sp., *Charops* sp., *Cardiochiles trimaculatus* and *Enicospilus* sp.) is illustrated in fig. 7. Each parasite occurs in both halves of the year, *Apanteles* and *Charops* being more common during the first half, from *Heliothis* on maize and groundnuts, and *Cardiochiles* and *Enicospilus* more common in the second half, from *Heliothis* collected mainly on cotton.

Conclusions.

It is evident from the data presented that *H. armigera* is active, at a low level, throughout the year, with no obvious seasonal fluctuations. In the crops examined, the populations built up with the development of the crop, oviposition starting one or two weeks before flowering and increasing to a maximum that coincided with the flowering peak. There was no evidence of population efflux from one crop to another, nor of maize or sunflower being more attractive to ovipositing moths than was adjacent cotton.

The cropping sequence practised at Namulonge is such that no crop in the succession overlaps a preceding crop. The period between successive crops is long

enough to ensure that the great majority of the pupae derived from a given crop will have emerged before the subsequent crop is attractive to the adults, thereby forcing the moths to seek food and oviposition sites elsewhere, that is, amongst the wild host-plants. This dispersal of the population possibly accounts for the low numbers initially encountered on the cultivated host-plants and the subsequent slow build-up within them.

The density of *H. armigera* and of *Earias* spp. at Namulonge is relatively low in comparison with other cotton areas in Africa, and they do not cause enough damage to affect the yield seriously over and above the variation caused by other environmental features. However, an assessment of the losses caused to June-sown cotton showed that an increase of seed cotton of up to 30 per cent. could be obtained following insecticidal control of late-season pests, mainly comprising *Heliothis* and *Earias* (Coaker, 1957). Nevertheless, the increases obtained were much lower in the majority of seasons investigated.

The main climatic differences between the Namulonge area in Uganda, having

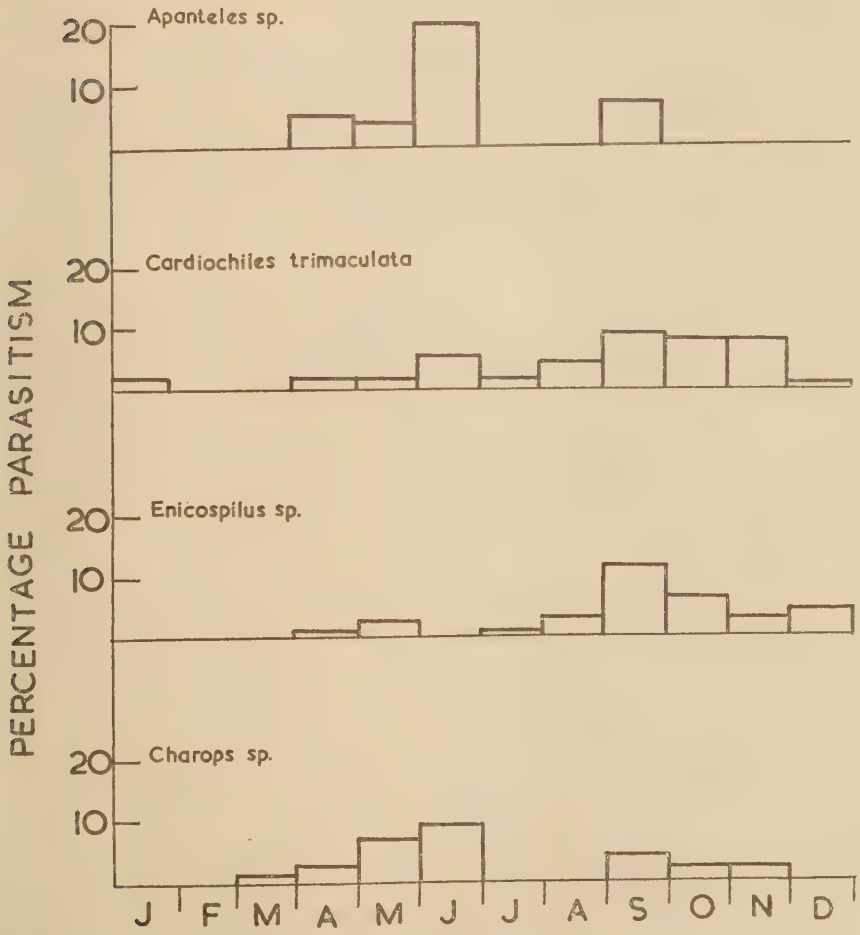


Fig. 7.—Mean percentage parasitism of *Heliothis armigera* by the four most common parasites, 1954–57.

low *Heliothis* densities, and areas where high densities are encountered, is the occurrence in the latter of a pronounced dry season, with low minimum temperatures. Under such conditions, the populations of *Heliothis* vary greatly during the year, and are low during the dry season, when resting or diapausing pupae are more common. The onset of emergence from the latter coincides with the start of the rainy season and a new growth cycle of both wild and cultivated host-plants; under such conditions, rapid development of *Heliothis* populations is common, and is emphasised by the migration of populations from early- to late-sown crops, which often overlap.

At Namulonge, parasitism was low in most cases, as compared with the parasitism rates determined in South Africa by Parsons (1940*a*), but this is possibly to be expected in view of the lower over-all numbers of *Heliothis*. No less than 17 species of egg or larval parasites were recorded, together with a nuclear polyhedral virus that infected the larvae. Although no estimation of the mortality rate inflicted by the disease was made owing to the low numbers of diseased larvae found (Coaker, 1958), infected larvae were more noticeable during times of abundant rainfall.

It can be concluded that the most important features of the environment at Namulonge, as regards the levels of infestation of cultivated crops by *Heliothis armigera*, are those that affect the seasonal activity of *Heliothis* in such a way that no resting or diapause phase is induced. Two such factors are temperature and rainfall. Continuous activity of *Heliothis* therefore occurs, as has been demonstrated on a succession of cultivated host-plants, and the population remains relatively stable throughout the year, possibly being maintained as such by a well balanced parasite-host relationship.

Summary.

A survey of the populations of eggs and larvae of *Heliothis armigera* (Hb.) was made on the Cotton Research Station, Namulonge, in Buganda Province, Uganda, over the four-year period, 1954–57 inclusive, on cotton, maize, groundnuts, beans and, in one year, sunflower. The populations encountered were low in comparison with some other cotton areas in Africa. The oviposition rate on each crop closely followed the flowering cycle, and there was no indication of the population from one crop influencing that on a subsequent crop, even when their flowering cycles overlapped. Under the normal crop sequence there is a sufficient gap between the attractive phases of successive crops to cause dispersal, possibly to wild host-plants, of the moths emerging from pupae bred in the preceding crop.

The variation in population from year to year on a given crop was no greater than that between different localities in any one season. Maize and sunflower did not prove successful when tested as trap crops grown adjacent to cotton.

Earias spp. and *Argyroploce leucotreta* Meyr. were less abundant than *Heliothis* and together constituted only 27 per cent. of the total population of Lepidopterous larvae on cotton.

A method is described for breeding *H. armigera* in the laboratory, in which the mean duration of the various stages was: egg, 4 days; larva, 24·8 days; pupa, 22·9 days; preoviposition period, 3·1 days; and oviposition period, 10·4 days. The mean number of eggs laid per female was 751·6, of which 71·4 per cent. hatched. Larval diets consisting of differing species and parts of food-plants caused significant differences in larval and pupal periods, the former being least (21·8 days) on maize silks and greatest (33·6 days) on sunflower corolla and receptacle, and the latter least (19·7 days) after larval feeding on three-week-old maize cobs and greatest (26 days) after seven-week-old cotton bolls. Pupae developing from larvae collected from the field did not exhibit any diapause or resting stage.

Two egg parasites and 15 larval parasites (three of which were probably secondary) were bred from material of *H. armigera* collected in the field, but the degree of parasitism remained low throughout the year. A nuclear polyhedral virus disease of the larvae was also recorded.

It is concluded that under the climatic conditions encountered, *H. armigera* is active throughout the year because wild or cultivated food-plants are always available and no resting stage of the insect is induced; this continuous activity is accompanied by biologically controlling factors that maintain populations stable at a relatively low level.

Acknowledgements.

My thanks are due to the Commonwealth Institute of Entomology for the identification of the parasites mentioned. I also gratefully acknowledge the opportunity of discussing the subject-matter of this paper with Mr. E. O. Pearson.

References.

Andrewartha, H. G. & Birch, L. C. (1954). The distribution and abundance of animals.—782 pp. Chicago, Ill., Univ. Chicago Pr.

Barber, G. W. (1936). The cannibalistic habits of the corn ear worm.—*Tech. Bull. U.S. Dep. Agric.* no. 499, 18 pp.

Coaker, T. H. (1957). Studies of crop loss following insect attack on cotton in East Africa. II. Further experiments in Uganda.—*Bull. ent. Res.* **48** pp. 851–866.

Coaker, T. H. (1958). Experiments with a virus disease of the cotton bollworm *Heliothis armigera* (Hbn.).—*Ann. appl. Biol.* **46** pp. 536–541.

Ditman, L. P., Weiland, G. S. & Guill jr., J. H. (1940). The metabolism in the corn earworm. III. Weight, water and diapause.—*J. econ. Ent.* **33** pp. 282–295.

Hutchinson, Sir J., Manning, H. L. & Farbrother, H. G. (1958). Crop water requirements of cotton.—*J. agric. Sci.* **51** pp. 177–188.

Jones, E. P. (1936). Investigations on the cotton boll worm, *Heliothis obsoleta*, Fabr.—*Publ. Brit. S. Afr. Co.* no. 4a pp. 21–82.

Jones, E. P. (1937). The overwintering pupa of *Heliothis armigera*, Hubn. (*obsoleta*, Fabr.).—I. Effect of temperature and moisture.—*Publ. Brit. S. Afr. Co.* no. 6a pp. 19–36.

McKinlay, K. S. (1956). Cotton pests in the Eastern Province, Tanganyika Territory.—*Emp. Cott. Gr. Rev.* **33** pp. 282–287.

McKinlay, K. S. (1957). Control of cotton pests in the Western Province, Tanganyika Territory.—*Emp. Cott. Gr. Rev.* **34** pp. 93–98.

McKinlay, K. S. & Geering, Q. A. (1957). Studies of crop loss following insect attack on cotton in East Africa. I. Experiments in Uganda and Tanganyika.—*Bull. ent. Res.* **48** pp. 833–849.

Manning, H. L. (1956). The statistical assessment of rainfall probability and its application in Uganda agriculture.—*Proc. roy. Soc.* (B) **144** pp. 460–480.

Marshall, J. (1936). The distribution and sampling of insect populations in the field with special reference to the American bollworm, *Heliothis obsoleta* Fabr.—*Ann. appl. Biol.* **23** pp. 133–152.

MICHELMORE, A. P. G. (1955). Annual report, Section of Entomology.—*Rep. Dep. Agric. Uganda 1954* pp. 114–118.

MICHELMORE, A. P. G. (1956). Annual report, Section of Entomology.—*Rep. Dep. Agric. Uganda 1955* pp. 167–176.

PARSONS, F. S. (1939). Investigations on the cotton bollworm, *Heliothis armigera* Hübn. (*obsoleta*, Fabr.). Part I. The annual march of bollworm incidence and related factors.—*Bull. ent. Res.* **30** pp. 321–338.

PARSONS, F. S. (1940*a*). Investigations on the cotton bollworm, *Heliothis armigera*, Hübn. (*obsoleta*, Fabr.). Part II. The incidence of parasites in quantitative relation to bollworm populations in South Africa.—*Bull. ent. Res.* **31** pp. 89–109.

PARSONS, F. S. (1940*b*). Investigations on the cotton bollworm, *Heliothis armigera*, Hübn. Part III. Relationships between oviposition and the flowering curves of food-plants.—*Bull. ent. Res.* **31** pp. 147–177.

PARSONS, F. S. & ULLYETT, G. C. (1934). Investigations on the control of the American and red bollworms of cotton in S. Africa.—*Bull. ent. Res.* **25** pp. 349–381.

PEARSON, E. O. (1950). Field key to the principal disorders of cotton in Africa. —*Emp. Cott. Gr. Rev.* **27** pp. 10–15.

RAINEY, R. C. (1948). Observations on the development of the cotton boll, with particular reference to changes in susceptibility to pests and diseases.—*Ann. appl. Biol.* **35** pp. 64–83.

TOTHILL, J. D. Ed. (1940). Agriculture in Uganda.—551 pp. Oxford, Univ. Pr.

VALENTINE, E. W. (1955). Entomology.—*Progr. Rep. Exp. Stas Emp. Cott. Gr. Corp. 1953–54* Tanganyika (East. Prov.) pp. 6–10.

VALENTINE, E. W. (1956). Entomology.—*Progr. Rep. Exp. Stas Emp. Cott. Gr. Corp. 1954–55* Tanganyika (East. Prov.) pp. 10–14.

© Commonwealth Agricultural Bureaux, 1959.

THE EFFECT OF CLIMATE AND WEATHER ON THE NUMBERS OF THE RED LOCUST, *NOMADACRIS SEPTEMFASCIATA* (SERV.), IN THE RUKWA VALLEY OUTBREAK AREA.

By P. Symmons

International Red Locust Control Service, Abercorn, Northern Rhodesia.

On three occasions during the past century, Africa has suffered from widespread and prolonged plagues of the red locust, *Nomadacris septemfasciata* (Serv.) (Gunn, 1952). The most recent of these lasted from 1929 to 1944 and almost the whole of Africa south of the Equator was affected during that time (Morant, 1947). During the thirties it was suggested that the red locust breeds in large numbers and forms initial swarms in a few favoured regions only, and that swarms from these outbreak areas start plagues. The widespread occurrence of plague swarms made the discovery of the outbreak areas difficult, but the work of Allan (1931), Harris (1933), Michelmore (1936) and Lea (1938) made possible the identification of two such areas, the Rukwa Valley of south-west Tanganyika, and Mweru wa Ntipa in Northern Rhodesia. These regions are level grass-covered plains which may be dry or may be largely covered with a foot or more of standing water during the wet season. Both are basins of inland drainage and both contain shallow saline lakes of fluctuating area. Subsequently, many isolated areas of similar type have been visited (Vesey-FitzGerald, 1953*a*, *b*, 1954*a*, 1955) but with the exception of part of the Malagarasi drainage basin in western Tanganyika, no other outbreak areas have been found.

The simplest way to combat the red locust is to prevent the escape of swarms from the outbreak areas, since if no swarms escape, a plague cannot start. When the locust population is small, swarms are unlikely to form, but when it is large, swarms will occur and an escape is always possible. If the population is to be kept at a safe level cheaply it would be most valuable to be able to predict the fluctuations in the numbers of locusts so that arrangements on the appropriate scale could be made in advance.

The Life-cycle of the Red Locust.

The red locust exists in its outbreak areas under a strongly contrasted seasonal régime. From May to October inclusive, little or no rain falls and the temperature mounts steadily, reaching 100°F. on many days in October and November. During this time the locusts are adult. The first isolated rain-storms often occur in October, and in November some rain has always been recorded. Using the criterion put forward by Chaplin (1954), namely that " the first day in a period of 4 days on at least 3 of which more than 0·01 in. of rain was recorded, the total rain for the period being 0·40 in. or more " shall be regarded as the start of the rainy season, the start of the rains at one station in the area, Kafukola, has varied between 5th November and 1st December during a 5-year period. With the start of the rains the maximum daily temperature falls and egg-laying by the red locust takes place. After a four-week incubation period the first hoppers emerge; this occurs usually about the end of the year (Robertson, 1958; Gunn, 1953, 1954, 1955*b*, 1956*b*, 1957); there is only one egg-laying period, though up to three pods, each containing about one hundred eggs, may be laid (Robertson, 1954). Given ideal conditions, the multiplication at breeding could be over a

hundred times, but the highest estimated has been about 45 times and the lowest $1\frac{1}{2}$ times. It is obvious that the success of breeding will have a great effect on the size of the subsequent adult locust population and consequently on the possibility of an outbreak. During the breeding period the adults start to die, although there may be some earlier wastage, and none survives the rainy season. In February or early March the first new adults appear (Gunn, 1953, 1954, 1955*b*, 1956*b*, 1957).

The locust lays its eggs a few inches deep in the ground. It is thought that rather special conditions are needed for successful incubation and that a soil that is neither dry nor waterlogged but moist is required (Faure, 1935); it is not known exactly what climatic conditions produce such a soil.

Climate and Numbers of the Red Locust.

No outstandingly important biological factor affecting numbers of the red locust is known. Total population within the outbreak areas used to be reduced by emigration of swarms, which is generally accepted as being density dependent (Nicholson, 1948). Today the main known killer of locusts is man, but big fluctuations, due to other causes, do occur and it seems self-evident that climate and weather, acting either directly or indirectly, must be amongst those causes. Gunn (1955*a*, 1956*a*) has suggested that either an extensive lake or heavy rainfall can lead to unsuccessful breeding in the outbreak areas. There is also evidence that drought at the time of egg-laying may reduce breeding success. In 1952, eggs dried up in the ground in Central Rukwa (Albrecht, 1956). Recently, Robertson (1958) has provided evidence that, within the Rukwa Valley, a critical drop in temperature appears to be necessary before ovarian development can take place. The date of this drop could influence the extent of multiplication. Lastly, the size of the parent population must affect the size of the resulting hopper population.

The appropriate data are available for the Rukwa Valley region only. For this region, an attempt has been made to estimate the effect of five factors on the numbers of the red locust: (a) the level of Lake Rukwa; (b) the amount of the early rainfall; (c) the total rainfall for the season both within the outbreak area and over the drainage basin; (d) the size of the parent population; and (e) the date of the critical drop in temperature which appears to be associated with the start of ovarian development.

Data and Treatment of Data.

Data concerning the level of Lake Rukwa and numbers of locusts in the valley have come, until recently, from eye-witness accounts only. Some sort of estimate of the lake level is available for each year after 1930, except only for 1943, and there are descriptions of locust numbers for each year after 1937 (Gunn, 1956*a*). The reports for the early years of the period possibly underestimate the numbers of locusts, since much of the area was virtually inaccessible and therefore unknown at that time. Assigning a quantitative value to eye-witness accounts is both difficult and unsatisfactory. I have, however, reviewed many of the original sources (Bredo, 1947, 1948, 1949, 1951, 1952; Vesey-FitzGerald, 1950; Gunn, 1953, 1954, 1955*a*, 1956*a*, 1957) and attempted to place the reports in a relative scale and have been able to divide lake level and adult infestation into five states. The estimates for lake level and locust infestation are shown graphically in fig. 1 and fig. 2, A, respectively. Up to 1947, when adults began to be controlled by insecticides, the size of the parental population * has been taken, in general, as

* The population immediately after fledging has been termed the filial population; that present in the middle of the dry season, the adult population; and that present at the time of oviposition, the parental population.

being proportional to the size of the adult population of the middle of the dry season, though this may be decidedly inaccurate (Scheepers & Gunn, 1958).

Rainfall information is available for the Rukwa Valley from observations kept by the Service since 1950–51; the number of stations in operation has increased from 2 in 1950–51 to over 30 in recent years. In addition, observations are available from the White Fathers' Missions at Mamba and Zimba near the steep south-west escarpment, Galula and Rukwa Hotel (Msisikaunga) in the south-east, and Sumbawanga on the plateau to the west of the valley. Unfortunately none of the records from these stations is complete. In addition, judging from recent years, the falls for Mamba and Zimba are higher than those for the valley. This view is supported by evidence from three Service stations situated, respectively, about 300 ft. up the scarp slope, at the scarp foot, and 5 miles from the escarpment in the plains. Records for three years show that the escarpment station has consistently higher rainfall than that on the plains, as much as double the amount having been recorded at the former as at the latter in one season. On the other hand, rainfall at Galula and Rukwa Hotel tends to be less than in the plains. The seasonal rainfall in the valley has been obtained by using all the records available for a given season but adjusting the total, where stations are included whose seasonal rainfalls differ from those of the valley, by the mean difference in seasonal total between these stations and the valley, judging from the period 1950–51 to 1956–57. The average rainfall for October, November and December for each year has also been found. Rainfall in the Rukwa Valley, estimated thus for the period 1940–41 to 1955–56, is shown in fig. 2, C.

The annual rainfall figures for the Rukwa drainage basin are more satisfactory (fig. 2, B). In 1937, there were returns from 11 stations scattered over the area and scanty records are available back to 1927. In recent years over 30 stations have been functioning.

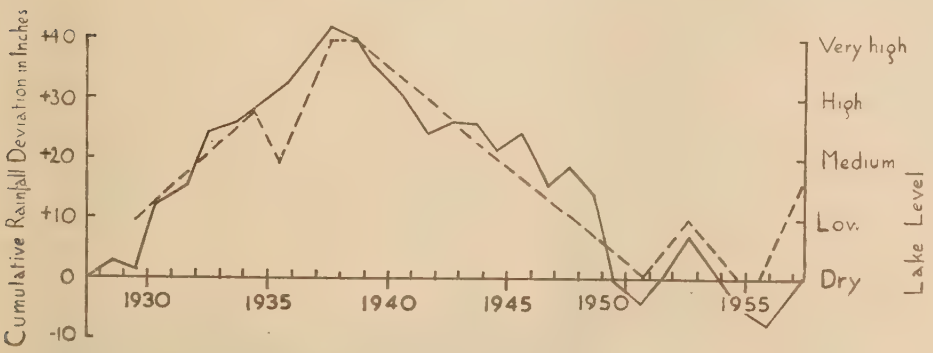


Fig. 1.—Correlation of rainfall and level of Lake Rukwa, Tanganyika. Cumulative deviation from mean rainfall over the Rukwa drainage basin (taken as 38 in.), solid line. Lake level (arbitrary scale), dotted line. The values are those at the end of the rainy season terminating in the year denoted by the figure to the left of the space representing the year (*e.g.*, the maximum rainfall deviation and maximum lake level were reached in mid-1937, at the end of the 1936–37 rainy season).

Lake Level and Locust Numbers.

From 1930 to 1937 the cumulative excess of rainfall (see p. 517) increased every year and the lake rose to a very high level (fig. 1). There is little information about the locusts up to 1936; after 1936, eye-witness reports are available for each year, though the early estimates are not very reliable.

From 1937 to 1942, the lake level was still exceptionally high and local reports indicate that no unflooded grass plain existed, even in the dry season, outside the forest at Milepa. The plains everywhere in the valley must have been small and waterlogged, although increasing in area and drying out as the cumulative excess of rainfall diminished and the lake receded. In all this period, locust numbers were consistently low until they rose in 1942. Because of the very high lake level reached in 1937, even the fact that the rainfall was not above average in the

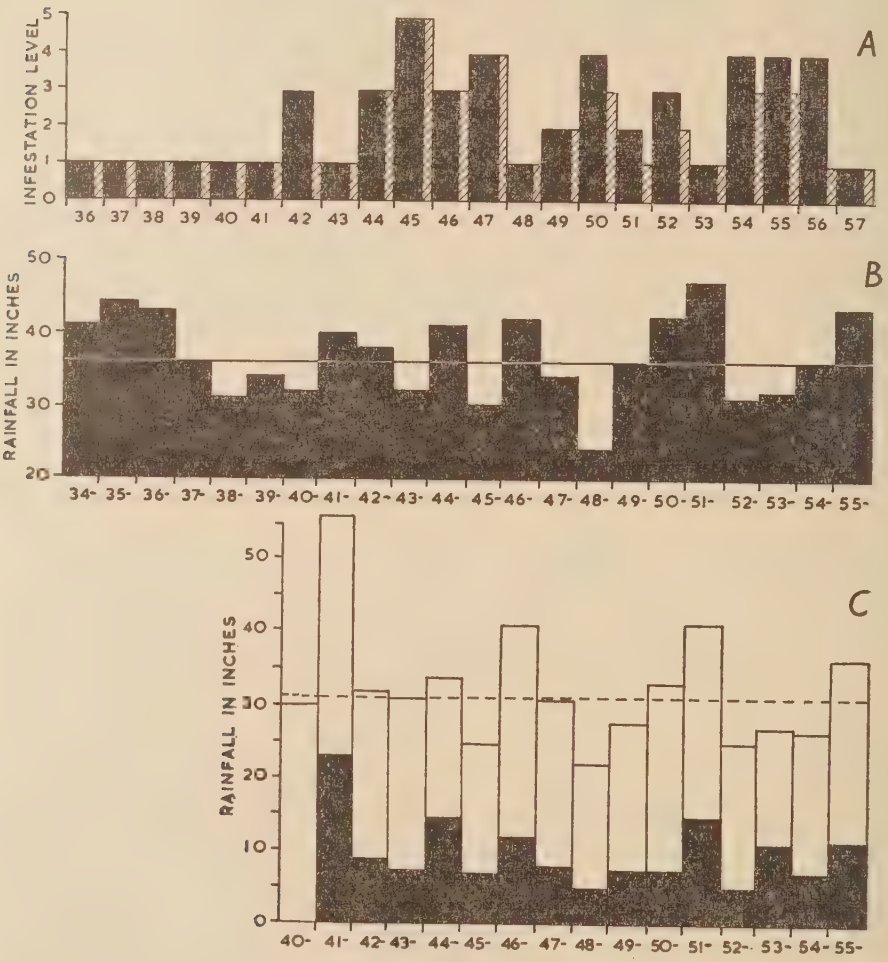


Fig. 2.—Rainfall and infestations of red locust, Lake Rukwa, Tanganyika. A. Level of infestation of red locust (on arbitrary scale) in years 1936 to 1957 : adult population in mid-year, solid bars; parent population near end of year, shaded bars. B. Rainfall over Rukwa drainage basin, 1934–35 to 1955–56. C. Rainfall over Rukwa Valley, 1940–41 to 1955–56; total rainfall indicated by height of open bar, early rainfall (October–December) indicated by height of solid bar. This figure is arranged so as to show the relationship between the rainfall in any given season (*e.g.*, 1940–41) and the size of the locust infestation in the next but one adult locust season (*e.g.*, 1942). The mean annual rainfall shown for the drainage basin (36 in.) is slightly lower over the period concerned (1934–1956) than the value (38 in.) used in fig. 1 for the period 1927–1957.

four subsequent rainy seasons did not result in the plains' becoming passable, as they have been in the dry season of most years since then. Obviously, the locusts cannot breed in large numbers if the area of suitable ground is small.

From 1942 onwards, by contrast, the unflooded grass plains became extensive during the dry season as the lake level fell, and their suitability for survival and breeding is worthy of further investigation. Certainly the size of the locust population fluctuated. Admittedly the area covered by water varied considerably from year to year, but the grass plains unflooded at the end of the dry season were always far more extensive than during the period of high lake level.

Rainfall and Locust Numbers.

There is no obvious connection, during the period 1942 to 1957, between the size of the parent population, filial population size, wet-season drainage-basin rainfall, wet-season Rukwa Valley rainfall, and early season valley rainfall. However, there is a striking relationship between the size of the adult locust population in a given year and the rainfall of the *season before* the most recent breeding season (fig. 2, A–C). When rainfall is heavy, either in the valley or over the drainage basin, the current parental population and the filial population

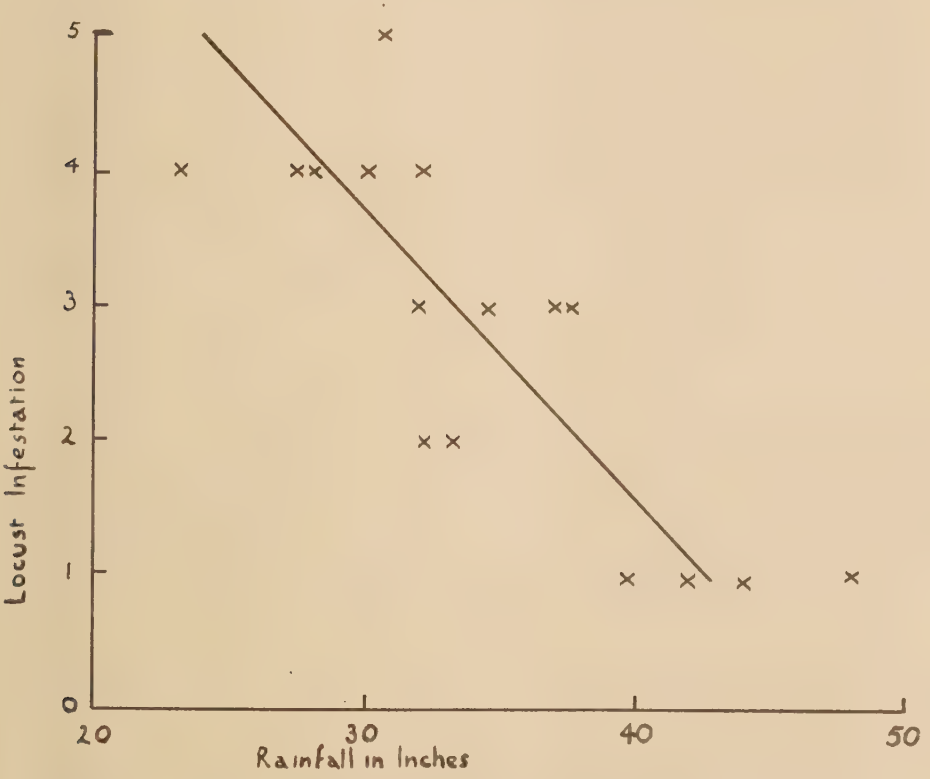


Fig. 3.—Correlation of rainfall and red locust infestation, Lake Rukwa, Tanganyika. Mean value of rainfall over Rukwa Valley and drainage basin in a given wet season plotted against level of adult locust infestation (on arbitrary scale) in the next but one dry season. The rainfall in July 1940–June 1941 is thus plotted against the level of adult infestation present about June 1942.

immediately following seem unaffected but *few* locusts result from *the next* season's breeding. When rainfall for the season is *low*, *many* locusts are found after the *next* breeding. Rainfall of average amount is followed by a breeding which produces a locust population of intermediate size. Fig. 2 is so arranged that the locust information lies above the seasonal rainfall total with which it bears this relationship; it can be seen how, when the seasonal rainfall total is high, subsequent locust infestation is low and *vice versa*. The regression of locust infestation on the rainfall of the last but one wet season for the Rukwa

TABLE I.

Relationship between adult population of red locusts and rainfall of last but one wet season.

Year	Rainfall (in.)		Mean of rainfall of Rukwa Valley and of drainage basin (in.)	Second following dry season	Adult population in that season*
	Rukwa Valley	Rukwa drainage basin			
1941–42 ..	56	40	48	1943	1
1951–52 ..	41	47	44	1953	1
1946–47 ..	41	42	42	1948	1
1955–56 ..	36	43	40	1957	1
1950–51 ..	33	42	38	1952	3
1944–45 ..	34	41	38	1946	3
1942–43 ..	32	38	35	1944	3
1947–48 ..	31	34	33	1949	2
1949–50 ..	28	36	32	1951	2
1940–41 ..	30	34	32	1942	3
1954–55 ..	27	36	32	1956	4
1943–44 ..	31	32	31	1945	5
1953–54 ..	27	32	30	1955	4
1952–53 ..	25	31	28	1954	4
1945–46 ..	25	30	28	1947	4
1948–49 ..	22	24	23	1950	4

* Adult population in mid dry season estimated on an arbitrary scale of 1—5.

Valley and the drainage basin are both highly significant (fig. 3). There is no way, as yet, of determining which has the greater effect on changes in the size of locust populations. The average rainfall of the drainage basin and valley has been found and the relationship of this value with adult locust infestation resulting from the next breeding is shown in Table I.

The Effect of Temperature on Breeding of the Red Locust.

A possible criterion for the start of ovarian development.

Robertson (1958) has suggested that ovarian development is associated with a drop in daily maximum temperature. His observations were made over three years and it was found that ovarian development began at some point during the following falls in maximum daily temperature; 38 to 27°C. in five days, 37 to 30°C. in six days, and 41 to 30°C. in four days. Before one of these falls, a maximum day temperature as low as 31°C. had been experienced for a short period, and some development did occur; on the other hand, a temporary reduction to 35°C. had no effect. The actual maximum temperatures on the days when development was first observed were 34, 30 and 28°C. It should be noted that showers and even heavy storms may occur before this drop in temperature and that general rain may be delayed or may be seriously interrupted afterwards. The correlation does appear to be with the temperature drop and not with the rainfall.

It is probable that there is an association between the start of ovarian development and a fall in maximum daily temperature. It seems that optimum conditions for the start of development are associated with a fall in maximum daily temperature from 37 to 30°C. in five days and minimum conditions with a fall from 35 to 31°C.

Application of the criterion.

A drop in temperature of the necessary range does take place at the start of nearly every rainy season. This drop shows three important characteristics: (a) it occurs simultaneously over a wide area; thus, in the 1956 records, the drop at Kafukola can be traced at Muse and Tumba, 40–50 miles away but also within the Rukwa Valley, whilst the drops for the years 1952 to 1956 at Kafukola can all be traced in the Mbeya records even though Mbeya is much higher and is about 150 miles away; (b) it occurs at the start of the rainy season, though it is not always associated with an actual rainstorm and is probably the result of widespread cloud and the extension of the cooler wet-season air mass; and (c) there is, as a rule, only one widespread drop in temperature. There are sometimes purely local falls in temperature, however, which are sufficient to permit some degree of ovarian development.

Estimation of Temperature of the Valley from Mbeya Data.

Correlations of maximum temperature for the 28-day period straddling the main drop in temperature at Kafukola and data for the same period at Mbeya give highly significant positive results for all the years 1952 to 1957. Transforming the Mbeya data to fit the higher Kafukola mean, the dates of the drops in temperature likely to have been associated with ovarian development have been estimated back to 1943. These drops in temperature can be taken as having occurred over the whole valley, though it must be remembered that earlier minor local drops, sufficient to permit some development and not reflected in the Mbeya data, may have taken place.

Possible Effect of the Date of the Drop in Temperature on Breeding Success.

The time of occurrence of the drop in temperature which is thought to be associated with ovarian development may, in some degree, affect breeding success. Egg-laying is associated with the end of the natural life of the parents. Robertson (1958) found that the natural decrease in numbers of adults in a 25 square-mile observation area sometimes started substantially before egg-laying and sometimes later. If the time of the decline in numbers of adults is not correlated with the date on which ovarian development starts, and there is nothing to suggest that it is, we would expect, over a long period, that the later this date the greater

would be the proportion of locusts which died without laying. Moreover, if, as has been suggested by Gunn (1956*a*), flooding limits breeding success, the later the start of ovarian development, the greater, in the long run, will be the chance of surface flooding occurring before the eggs hatch, and this might have a detrimental effect on embryonic development. On the other hand, if ripe eggs appear at an early date, over a period of years there will be a greater chance of subsequent drought either causing the pod to dry up in the ground or forcing the locust to retain it's eggs or deposit them unsuitably for survival. Robertson (1958) considers that the locust can hold ripe eggs for at least a week, and Albrecht (1956) holds that a drought of about the same duration immediately following laying affects the eggs unfavourably. This is exceedingly hypothetical, but it is felt that an attempt to estimate the independent effect of the date of the drop in temperature, which is thought to start ovarian development, on subsequent filial numbers, is worth while (see below).

TABLE II.

Data for multiple regression of adult population on meteorological factors.

Year	Parental population[1]	Rainfall in last but one wet season[2]	Date of drop in temperature[3]	Early season rainfall[4]	Adult population[5]
1942 ..	1	32	4	23	3
1943 ..	1	48	7	9	1
1944 ..	1	35	4	7	3
1945 ..	3	31	9	15	5
1946 ..	5	38	8	7	3
1947 ..	3	28	9	12	4
1948 ..	4	42	7	8	1
1949 ..	1	33	13	5	2
1950 ..	2	23	1	8	4
1951 ..	3	32	7	8	2
1952 ..	1	38	13	15	3
1953 ..	2	44	9	5	1
1954 ..	1	28	9	11	4
1955 ..	3	30	9	7	4
1956 ..	3	32	9	11	4
1957 ..	1	40	8	7	1

[1] Estimated size of parental population (on an arbitrary scale of 1—5) at the time of oviposition in the year previous to that given.

[2] Mean of the rainfall in the Rukwa Valley and the Rukwa drainage basin in the last but one wet season (in.).

[3] Expressed as number of weeks between 4th October and date of the drop in temperature believed to initiate ovarian development.

[4] Rukwa Valley rainfall in previous October–December.

[5] Adult population in mid dry season of the year given (on an arbitrary scale of 1—5).

Statistical Analysis.

For the period 1942 to 1957, inclusive, a statistical analysis of the data has been attempted. A multiple regression has been calculated involving the effect on the size of the adult population in mid dry season of: (1) the rainfall during the last but one wet season; (2) rainfall within the valley in the preceding October–December; (3) the date of the temperature drop that is thought to start ovarian development; (4) the size of the preceding parental population. The total rainfall for the relevant wet season has been taken as the mean value for the rainfall in the valley and over the drainage basin. This has been done since the water accumulating within the valley must depend on both direct rainfall and inflow of drainage water; as a first approximation it has been assumed that equal contributions are received from the two sources (see below). The data on which the calculations are based are given in Table II.

The following conclusions can be drawn from these calculations: the independent regression on the size of the adult population in mid dry season of (1) the rainfall during the last but one wet season is negative and highly significant ($P<0{\cdot}01$); (2) the amount of rain in the preceding October-December is positive and approaches significance ($P>0{\cdot}02<0{\cdot}05$); (3) the date of the drop in temperature, thought to start ovarian development, is negative but not significant ($P>0{\cdot}3<0{\cdot}4$); (4) the size of the preceding parental population is positive and significant ($P = 0{\cdot}01$).

We may eliminate the non-significant factor, namely the date of the temperature drop thought to start ovarian development. The resulting regression equation is:

$$y = 6{\cdot}518 - 0{\cdot}160x_1 + 0{\cdot}425x_2 + 0{\cdot}092x_3$$

where y = adult locust population in mid dry season,
x_1 = mean of the rainfall, in inches, of the Rukwa Valley and drainage basin during the last but one wet season,
x_2 = the infestation level of the breeding population,
x_3 = the rainfall of the Rukwa Valley, in inches, in the preceding October–December.

The total correlation is very significant ($R = 0{\cdot}93$, $P<0{\cdot}01$); the standard error of estimate is 0·55 unit in the scale of infestation levels.

Practically all the data on which this analysis is based are unsatisfactory in some degree; reliable information is now being accumulated so that in the future a more reliable estimate of the level of locust infestation should be possible.

Tentative Explanation of the Effect of Annual Rainfall and Lake Level on Locust Numbers.

A large annual rainfall gives rise, 18 months later, to a small adult population. This could be due to unsuccessful breeding. On the other hand it could be caused by a fall in parental locust numbers before breeding or in hopper and fledgling numbers after breeding. Let us examine the first possible explanation.

One important factor which could reflect the level of the previous season's rainfall at the end of the subsequent dry season is the water-table (Gunn, 1955*a*, 1956*a*). If we suppose that early flooding is the mechanism by which breeding success is reduced, we are faced with the problem of explaining how a high water-table can give rise to rapid flooding. A series of boreholes sunk in North Rukwa in 1954 showed the water-table to be 20 to 25 ft. below the surface about ten miles from the lake edge while at four miles from the shore it was 10 to 15 ft. down; this was after a series of years of low rainfall. It appears possible that the water-table reaches the surface at the shore of Lake Rukwa, the lake being an exposed part of the water-table. The lake edge is taken as that shown on the Preliminary Plot maps of the Directorate of Colonial Survey which are based on

aerial photographs taken in 1947 when the lake was more extensive than in 1954.

At the end of the dry season of 1957 the water-table was only 10 ft. below the surface 10 miles from the actual lake shore and at 3 miles from the lake edge a soil tensiometer recorded an increase in soil moisture one foot below the surface. At the end of a dry season following a season of heavy rainfall, saturated soil may exist at a depth of less than 10 ft. The average amount of rain received before the first hatching is about 10 in. Though this would be sufficient to saturate the soil it is unlikely that water could percolate sufficiently rapidly to build up directly on the water-table. However, capillary action should bring moisture within a foot or two of the surface, and this effect should be most marked after heavy wet-season rainfall. Such moisture near the surface might reduce the number and depth of earth cracks which would otherwise absorb much of the early-season rainfall. Thus with a comparatively low early-season rainfall, given a high water-table, the surface might ' gum up ' rapidly and water would stand on the land. On the other hand it is possible that a large amount of rain before the end of the year may be correlated positively with the size of filial population and, presumably, with breeding success. Superficially it would seem that heavy early-season rainfall should increase, not counteract, the effect of heavy rainfall in the previous season and *vice versa*. However, a rainy season which started early would allow early laying. In general, it is likely that the earlier the laying the larger the numbers of locusts which would lay before dying. If rainfall were well distributed over a long period, ideal laying conditions might be produced although the total fall before the end of the year might be large. It is obvious that further investigation is needed to find: (1) under what conditions of soil moisture locusts lay most successfully; (2) what amount of rain and what sort of rainfall distribution produce such soil conditions.

With much standing water at the end of the wet season and with moist soil close to the surface until the end of the dry season, one would expect grass to grow unusually thickly after a season of heavy rainfall. The impression at the end of the 1957 dry season was that an abnormal amount of green fresh growth existed. Vesey-FitzGerald (1954*b*) has suggested that a dense grass mat reduces oviposition sites and so limits breeding success. Such a dense mat might easily be found following a season of rainfall above the average. Symmons & Carnegie (1959) have shown that the red locust, if given the choice, will avoid, for egg-laying, ground covered with standing grass.

What produces a high water-table ? The water-table height must be a function of both direct rainfall and inflow. Rainey, Waloff & Burnett (1957) have reviewed the data concerning losses by evaporation from various African lakes and have come to the conclusion that the loss from Lake Rukwa is probably between 60 and 75 in. a year. Sansom (1954) using Thornthwaite's equation has calculated the probable annual evapo-transpiration loss for an area in Tanganyika of the height of the Rukwa Valley as 54 in., though in view of the dense grass cover and the large amount of standing water often found on the plains during the wet season this may be an underestimate in the case of the Rukwa area. In a normal year, roughly half of the amount of water loss should thus come from the direct rainfall of about 30 in., leaving half to be supplied by inflow. The inflow will vary directly with some complex function of the rainfall over the drainage basin. We may say that the water-table height depends on annual rainfall of the drainage basin and valley, though the contributions from each source in years of abnormal rainfall cannot, at present, be evaluated.

In a period when rainfall fluctuates about the normal, the previous season's total will determine, very largely, whether or not the water-table is above or below the average height. It will also affect the size of the lake, though it is unlikely that, since 1942, the area of unflooded grassland at the end of the dry season has

ever been small enough to preclude successful breeding. Rainfall can also have an effect after one year and probably, though to a progressively diminishing degree, after two, three, or four years. A high water-table, and thus a high lake, should be the result of a series of years of above-average rainfall. The variations in lake level and also the cumulative deviation of drainage-basin rainfall from normal are shown in fig. 1. The latter is calculated by adding algebraically the excess or deficit of one year's rainfall to the algebraic sum of the excesses and deficits back to the beginning of the period. The lake reached its highest point in 1938 after ten years when rainfall averaged 4 in. a year above normal. The decline in lake level from 1938 to 1950 coincided with a predominantly dry period. This is not surprising, but the similarity of the graphs is remarkable.

One would expect a high lake level to be linked to a high water-table and thus to produce poor breeding. However, as has been pointed out above, the small numbers of locusts between 1938 and 1942 must have been, at any rate in part, simply a result of the large size of the lake. A lake of that magnitude must have covered, perennially, much of the locust-breeding plain. A lake of at least the size existing in 1941 would seem to be necessary in order to make successful breeding improbable. On the evidence of this period, a cumulative excess of about 28 in. of rain, achieved within a small number of years, would be required to achieve this.

Let us now consider changes in adult mortality as a possible explanation of the variation in the size of the locust population at a time of low lake level. The majority of estimates of the numbers of locusts have been made early in the dry season; for the period 1942 to 1957, of the 12 years when the estimate can be assigned to a definite period, 11 have been made in the months May to August, inclusive. After a season with above-normal rainfall, a drop in the size of the locust population between August and the time of egg-laying, or a drop in the size of the subsequent hopper and fledgling population, or both, would be needed to give rise to small locust numbers. The evidence for such changes is scanty. Reduction in population size without chemical control appears to have occurred in two years. Michelmore (1945) stated that swarms died out late in the dry season of 1942. In North Rukwa, in 1957, locust numbers fell from over 6½ million in May to between 2 and 4 million in October, and from 16½ million in April to 2½ million in October in Central Rukwa. These figures are based on Land-Rover scouting except for the estimate of the North and Central Rukwa populations of May and April 1957; these were made using a Swamp Skipper and so may not be strictly comparable with the other data. On the other hand, in 1953 and 1949, after seasons of rainfall below average, locust numbers were maintained until late in the dry season. The 1949 data are not very satisfactory but the 1953 estimates of the North Rukwa population were made by Land-Rover scouting.

Uvarov (1957) has pointed out that short-horned grasshoppers, in general, thrive under semi-arid conditions. Prolonged wetness may somehow cause heavy mortality. To test this possibility, population assessments will need to be continued for a number of years. At the same time the effects of climate and weather on multiplication at egg-laying, acting either directly or through the conditions of the soil and vegetation, must also be investigated, and such investigations have been planned.

Forecasting of Locust Numbers from Lake Level and Annual Rainfall.

I consider that it is possible to work out a practical method of forecasting infestation by the red locust, at least for the Rukwa Valley outbreak area, even though we do not understand why locust numbers vary. First of all, when the lake was permanent and extensive there were few locusts. An extensive lake must mean something above any level experienced in recent years. In the late

nineteen thirties, a local resident, the late Major Bousfield, used to go by motor-boat between the south-east of the South Lake and the west shore of the North Lake, using a dug passage across the intervening neck of land that may be what is now called the Iwana Channel (Gunn, 1956*a*). This journey would have been quite impossible at any time within the last ten years.

Simplifying the data for the years 1942–1957, inclusive, when the lake level had ceased to be high and dominant, we can say that locust infestation was heavy (levels 4 and 5) 18 months after the 5 wet seasons when the average fall for the valley and the drainage basin was 31 in. or less and was moderate or low (levels 1, 2 and 3) after 9 of the 10 wet seasons when the average fall was above 31 in. (Table I). On this basis it should be possible to predict whether or not infestation is going to be heavy, or moderate or low, 12 months in advance. Using the regression equation, stated above (p. 515), which allows for the effect of the size of the breeding population and the early-season rainfall, a more precise forecast of locust infestation can be made.

The hypothesis that the rainfall total for a season is negatively correlated with the size of the adult locust population 18 months later was first put forward late in 1956. The size of the adult populations for 1957 and 1958 have been forecast successfully. Relying on the forecast, control of locust hoppers was not mounted on a large scale in either 1956–57 or 1957–58. Great savings in expense have thus been achieved.

The total fall for the last but one rainy season is the most recent seasonal total that affects the breeding that produces a given adult population. It is somewhat surprising that the amount and distribution of the rain that falls whilst the egg-pods are in the ground appears to have so little effect. However, other workers have found a similar correlation. Lea (1958) has found that changes in the numbers of the brown locust, *Locustana pardalina* (Wlk.), are linked with the previous season's early summer rainfall, a dry early summer being followed by an increase and a wet early summer by a decrease in locust numbers in the next year. Smith (1954) has stated that, with grasshoppers in Kansas, outbreaks have followed two years in succession of sub-normal rainfall and that low numbers have occurred when rainfall has been above normal in a given summer and the year before.

Summary.

An examination of the records from 1930 onwards shows that a very high level of Lake Rukwa is correlated with small numbers of the red locust, *Nomadacris septemfasciata* (Serv.), in the Rukwa Valley outbreak area in Tanganyika. When the lake level is not very high, the size of the adult locust population (taken as that present in the middle of the dry season) is correlated negatively with the total rainfall of the last but one wet season (broadly, November–May), positively with the size of the preceding parental population (taken as that present at the time of oviposition) and possibly also with the rainfall of the preceding October–December, but not significantly with the date of the drop in temperature that is thought to be associated with the start of ovarian development.

Three tentative explanations of the correlation between adult population and rainfall are offered. First, if the water-table is high because of heavy rain in the previous season, the early rains may make the soil unsuitable for successful egg-laying and incubation; second, after a season of heavy rainfall the grass cover may be particularly dense at the end of the following dry season and the consequent reduction of the oviposition sites may make breeding unsuccessful; third, parental mortality may be high during a dry season following heavy rains. These possibilities are being further investigated.

It is suggested that by using a multiple regression equation incorporating the correlations that have been established, the size of the adult locust population

can be forecast in time for the scale of hopper control measures to be appropriately modified and economies thereby achieved.

Acknowledgements.

I should like to thank the members of the scientific staff of the International Red Locust Control Service for their help and advice. My special thanks are due to Dr. Gunn who initiated the work and who has given encouragement and assistance throughout.

References.

Albrecht, F. O. (1956). Limitation des effectifs chez un acridien: influence de la sécheresse du sol sur les oeufs de *Nomadacris septemfasciata* (Serv.).—*Locusta* no. 4 pp. 1–21.

Allan, W. (1931). Locusts in Northern Rhodesia.—*Annu. Bull. Dep. Agric. N. Rhod.* no. 1 pp. 6–11.

Bredo, H. J. (1947). Report on the control measures and their organisation against the Red Locust in the outbreak centres Mweru wa Ntipa and Rukwa since 1938.—60 pp., multigraph. (Unpublished.)

Bredo, H. J. (1948). Report on control measures and their organisation against the Red Locust 1947–48.—27 pp., multigraph. (Unpublished.)

Bredo, H. J. (1949). Report on control measures and their organisation against the Red Locust, 1948–49.—36 pp., multigraph. International Red Locust Control Service. (Unpublished.)

Bredo, H. J. (1951). Annual report of the International Red Locust Control Service for 1950–51.—58 pp., multigraph. (Unpublished.)

Bredo, H. J. (1952). Annual report of the International Red Locust Control Service for 1951–52.—19 pp., multigraph. (Unpublished.)

Chaplin, J. H. (1954). On the wet season in Northern Rhodesia.—*Weather* **9** pp. 272–275.

Faure, J. C. (1935). The life history of the red locust (*Nomadacris septemfasciata* (Serville)).—*Bull. Dep. Agric. S. Afr.* no. 144, 32 pp.

Gunn, D. L. (1952). The red locust.—*J. R. Soc. Arts* **100** pp. 261–284.

Gunn, D. L. (1953). Annual report of the Director of International Red Locust Control Service for 1952–53.—70 pp., multigraph. (Unpublished.)

Gunn, D. L. (1954). Report of the Director of International Red Locust Control Service for transitional period 1953.—27 pp., multigraph. (Unpublished.)

Gunn, D. L. (1955*a*). Mweru wa Ntipa and the Red Locust.—*N. Rhod. J.* **2** no. 6 pp. 3–15.

Gunn, D. L. (1955*b*). Annual report of the Director of International Red Locust Control Service for 1954.—57 pp., multigraph. (Unpublished.)

Gunn, D. L. (1956*a*). A history of Lake Rukwa and the red locust.—*Tanganyika Notes* no. 42 pp. 1–18.

Gunn, D. L. (1956*b*). Annual report of the Director of International Red Locust Control Service for 1955.—59 pp., multigraph. (Unpublished.)

Gunn, D. L. (1957). Annual report of the Director of International Red Locust Control Service for 1956.—67 pp., multigraph. (Unpublished.)

Harris, W. V. (1933). The red locust.—*Pamphl. Dep. Agric. Tanganyika* no. 10, 10 pp.

Lea, A. (1938). Investigations on the red locust, *Nomadacris septemfasciata* (Serv.), in Portuguese East Africa and Nyasaland in 1935.—*Sci. Bull. Dep. Agric. S. Afr.* no. 176, 30 pp.

Lea, A. (1958). Recent outbreaks of the brown locust, *Locustana pardalina* (Walk.), with special reference to the influence of rainfall.—*J. ent. Soc. S. Afr.* **21** pp. 162–213.

Michelmore, A. P. G. (1936). Economic Advisory Council. Committee on Locust Control. Locust investigation in Tanganyika.—Report no. 4, 64 pp., typescript. (Unpublished Report at International Red Locust Control Service.)

Michelmore, A. P. G. (1945). The International Red Locust Control.—*Tanganyika Notes* no. 20 pp. 1–7.

Morant, V. (1947). Migrations and breeding of the red locust (*Nomadacris septemfasciata* Serville) in Africa, 1927–1945.—*Anti-Locust Mem.* no. 2, 60 pp.

Nicholson, A. J. (1948). Fluctuations of animal populations.—*Rep. Aust. Ass. Adv. Sci.* **26** pp. 134–148.

Rainey, R. C., Waloff, Z. & Burnett, G. F. (1957). The behaviour of the red locust (*Nomadacris septemfasciata* Serville) in relation to the topography, meteorology and vegetation of the Rukwa Rift Valley, Tanganyika.—*Anti-Locust Bull.* no. 26, 96 pp.

Robertson, I. A. D. (1954). The numbers of eggs in pods of the red locust, *Nomadacris septemfasciata* (Serville) (Orth., Acrididae).—*Ent. mon. Mag.* **90** pp. 254–255.

Robertson, I. A. D. (1958). The reproduction of the red locust, *Nomadacris septemfasciata* (Serv.) (Orthoptera, Acrididae), in an outbreak area.—*Bull. ent. Res.* **49** pp. 479–496.

Sansom, H. W. (1954). The climate of East Africa based on Thornthwaite's classification.—*Mem. E. Afr. Met. Dep.* **3** no. 2.

Scheepers, C. C. & Gunn, D. L. (1958). Enumerating populations of adults of the red locust, *Nomadacris septemfasciata* (Serville), in its outbreak areas in East and Central Africa.—*Bull. ent. Res.* **49** pp. 273–285.

Smith, R. C. (1954). An analysis of 100 years of grasshopper populations in Kansas (1854 to 1954).—*Trans. Kans. Acad. Sci.* **57** pp. 397–433.

Symmons, P. & Carnegie, A. J. M. (1959). Some factors affecting breeding and oviposition of the red locust, *Nomadacris septemfasciata* (Serv.).—*Bull. ent. Res.* **50** pp. 333–353.

Uvarov, B. P. (1957). The aridity factor in the ecology of locusts and grasshoppers of the Old World.—*In* Arid zone research: human and animal ecology, pp. 164–198. Paris, UNESCO.

Vesey-FitzGerald, D. (1950). Annual report of the International Red Locust Control Service for 1949–50.—33 pp., multigraph. (Unpublished.)

Vesey-FitzGerald, L. D. E. F. (1953*a*). Report on a visit to the Kafue Flats. —16 pp., typescript. (Unpublished report at International Red Locust Control Service.)

Vesey-FitzGerald, L. D. E. F. (1953*b*). A visit to the Wembere.—21 pp., typescript. (Unpublished report at International Red Locust Control Service.)

VESEY-FITZGERALD, L. D. E. F. (1954*a*). Survey of red locust habitats and incidence in the Chambeshi Valley, Northern Rhodesia.—16 pp., typescript. (Unpublished report at International Red Locust Control Service.)

VESEY-FITZGERALD, L. D. E. F. (1954*b*). Fire control in red locust outbreak areas and a scheme for its application.—10 pp., typescript. (Unpublished report at International Red Locust Control Service.)

VESEY-FITZGERALD, L. D. E. F. (1955). Survey of red locust habitats and incidence in part of the Luangwa Valley, Northern Rhodesia.—12 pp., typescript. (Unpublished report at International Red Locust Control Service.)

© Commonwealth Agricultural Bureaux, 1959.

IMMATURE NUTFALL OF COCONUTS IN THE SOLOMON ISLANDS.

II.—CHANGES IN ANT POPULATIONS, AND THEIR RELATION TO VEGETATION.

By E. S. Brown

Commonwealth Institute of Entomology.

(Plates XII–XVI.)

Contents.

	PAGE
Changes in ant populations	525
Rapidly changing populations	525
Relatively stable populations	530
Ant battles	534
Types of vegetation associated with ant species	535
List of prevalent plants	535
Vegetation associated with *Oecophylla smaragdina*	538
Vegetation associated with *Anoplolepis longipes*	539
Vegetation associated with *Pheidole megacephala*	539
Vegetation associated with *Iridomyrmex myrmecodiae*	540
Vegetation associated with mixed ant populations	543
Experiments on vegetation	543
Vegetation control by 'brushing'	543
Transplantation of *Oecophylla* nests	547
Ant succession	548
'Background' terrestrial ant populations	555
Summary	556
Acknowledgements	557
References	557

In Part I of this series of papers (Brown, 1959) the evidence was discussed for the indirect dependence of immature nutfall of coconuts upon certain species of ants, some of which protect the palms against attack by the primary cause of nutfall in the British Solomon Islands Protectorate (the Coreid bug, *Amblypelta*, chiefly *A. cocophaga* China), while others do not.

Of a large number of ant species occurring in coconut plantations and foraging over the palms (Appendix B to Part I), only a small number are ever dominant, and since these tend to antagonise and exclude one another, only one of them is normally dominant on any one palm and even over quite large areas of a plantation. Thus a large area may be dominated on the one hand by *Oecophylla smaragdina* (F.) or *Anoplolepis longipes* (Jerd.), in which case there will be little or no nutfall since they give protection against *Amblypelta*; or on the other hand by *Pheidole megacephala* (F.) or *Iridomyrmex myrmecodiae* Emery in which case there may be a greater or lesser amount of nutfall since they give no protection.

Although usually one or other of these four species dominates an area, to the almost total exclusion of other species, there is frequently a tendency for the ant population to be mixed and to contain a larger proportion of economically less important indigenous species.

Since the content of the ant population is of such importance in relation to nutfall, it is of interest to know whether populations tend to remain stable or to change, and if they change, to know what factors influence the replacement of one species by another. Much attention has been given to this, in the hope that it might indicate cultural or other methods of changing populations in a direction favourable for protection of palms against nutfall.

There is already evidence that ant populations can sometimes change quite rapidly, and that local fluctuations in nutfall are largely dependent on such changes (O'Connor, 1950; Phillips, 1956). The author maintained observations over a period of 2½ years (May 1954 to November 1956) on a number of plantations, to find out among other things whether such far-reaching changes as those described by O'Connor and Phillips are of common occurrence, or whether the more usual condition is one of comparative stability.

The far-reaching changes referred to above involved, in the main, a replacement of *Pheidole* by *Oecophylla* in a group of plantations on the north coast of Guadalcanal (Kukum, Lunga and Tenaru); since these changes were accompanied by recovery from severe nutfall, great importance was attached to them, and attempts were made to explain their cause. Two rival explanations which may be referred to as the cover-crop, or creeper, theory and the spray hypothesis, respectively, were advanced. The former was brought forward by O'Connor and Leach as the result of investigations in 1948 (O'Connor, 1950). A critical summary of it was given by Phillips (1956, p. 581). The Guadalcanal plantations, like most others, had become very overgrown during the war, and not only cover crops such as *Centrosema* and *Pueraria*, but also many kinds of wild creepers had got out of control and frequently grown up the palm trunks and in extreme cases ascended to the palm crowns (Pl. XVI, fig. 2). *Pheidole* tends to concentrate at the base of the trunk, and to use the creepers as cover and to run up and down the trunk beneath them, while *Oecophylla* prefers exposed runways and moves up the outside of the creeper cover, thus avoiding conflict with *Pheidole*. When the trunks are free from creepers, *Oecophylla* cannot invade a palm occupied by *Pheidole* without contact being made between the two ants, in which case a battle develops. Thus creeper growth, by providing a 'by-pass' runway, is supposed to have enabled *Oecophylla* to invade palms and areas previously held by *Pheidole*, and the replacement was followed by recovery from nutfall.

The spray hypothesis is based on the fact that, during the war years, the American forces carried out routine aerial insecticide spraying for mosquito control all along that part of the Guadalcanal coast where the plantations concerned are situated. Phillips (1956), who for certain reasons was not satisfied with the creeper theory, sought to explain the change as the result of a differential effect of the insecticides on the ant species, suggesting that *Pheidole* was affected to a greater extent by the treatment, thus allowing *Oecophylla* to increase, relatively, and gradually to gain the upper hand. He did some experiments with DDT and chlordane which he claimed to demonstrate the differential effect necessary to produce such a result.

The author made a number of observations on changes in ant populations, some of which have a bearing on these two theories. The implication of the creeper theory is that where overgrown conditions and creepers are prevalent, *Oecophylla* should tend more often to be dominant. It seemed important to make a thorough study of the vegetation associated with all the major ant species, to see if the latter are influenced to any great extent by different plants and plant associations. Further, it was obviously important to extend such observations more widely through the islands than those of previous workers, whose studies had been largely confined to a few plantations in a limited area of Guadalcanal. These observations and the conclusions to be drawn from them will now be described and discussed.

Changes in Ant Populations.

Except in a few limited areas, there were insufficient data in 1954 to study changes in ant distribution in a precise manner. This requires careful periodic plotting of selected areas palm by palm, and such plots were only available for limited parts of the following plantations: Kukum, Lunga, Tenaru, Mamara and Rua Vatu on Guadalcanal; one small plot at Baunani on Malaita; and Faielau and Pepesala in the Russell Islands. These areas had first been plotted by O'Connor and Leach in 1948 (except the Malaita plot which was first recorded in 1951). They were re-examined by Phillips in 1952, and again by the author in 1954; at the same time, additional plots were recorded not only in other parts of Guadalcanal, but also on Malaita and other islands.

The methods of recording ant distribution by samples and plots have already been described (Brown, 1959). From these samples and plots most of the data on which this paper is based have been extracted.

Rapidly changing Populations.

Some examples will first be described of relatively rapid changes in the composition of ant populations—changes of a type which are actually or potentially of importance from the point of view of nutfall.

The Kukum/Lunga/Tenaru group of plantations (Guadalcanal).

The history of this important group of plantations, which are all in contact with one another, was described up to 1952 by Phillips (1956, p. 576), on the basis of his re-examination of those of Leach and O'Connor's plots that were still recognisable. The whole area had in pre-war days been subject to heavy nutfall and had been overrun by *Pheidole megacephala*. In 1948, Leach and O'Connor found a large measure of recovery from nutfall; *Oecophylla smaragdina* now dominated considerable areas of the plots; *Pheidole* was still well represented, but although its detailed distribution in pre-war days had not been recorded, there is no doubt that it had been reduced. In 1952, Phillips found *Pheidole* completely absent from such plots as he identified, but he also found that a fresh species, *Anoplolepis longipes*, had in large measure replaced *Oecophylla*. In 1954, the author found, in most plots, a continued increase of *Anoplolepis* at the expense of *Oecophylla*.

Complete figures for all plots for all the three years 1948, 1952 and 1954 cannot be given, because although the author in 1954 managed to identify 16 of Leach and O'Connor's 18 plots in these plantations, Phillips in 1952 had identified and recorded figures for only seven of these, and also for one additional one (KB) which was unidentifiable in 1954 and must therefore be omitted. Furthermore, for two of these seven plots (KC and KE.1) Phillips only recorded a fraction of the number of palms included in 1948 and 1954. Thus it is only for five plots that comparable figures can be given for all three years. It is therefore proposed to give two separate sets of figures (Table I):—

(1) Combined figures for all the 16 plots identified in 1954, for the years 1948 and 1954.

(2) Combined figures for all three years, 1948, 1952 and 1954, for the five plots for which complete and comparable figures are available.

The first set indicates the magnitude of the total change over the whole 6-year period; the second shows also an intermediate stage in the change for a limited number of the plots.

The decrease in the total numbers of palms in 1952, and again in 1954, is accounted for by two factors: first, the falling of a number of palms during the period owing to a combination of old age and the delayed effect of war damage; secondly, the fact that in the 1948 figures for plots containing *Oecophylla* and

Pheidole, Leach recorded palms either as "with Oecophylla", or "without Oecophylla", and although the latter have been assumed to have been occupied by *Pheidole*, it is by no means certain that this was always the case, although it probably was for the most part; in 1954, other species of ants of minor importance were found in occupation of a few palms, and the omission of these from the figures in Table I is responsible for a slight reduction in total numbers of palms.

TABLE I.

Numbers of palms of which the crowns were occupied by the four principal ant species in certain plots in the Kukum/Lunga/Tenaru group of plantations (Guadalcanal) in the years 1948, 1952 and 1954.

Number of plots	Species of ant	Number of palms occupied			Total gains (+) or losses (−)
		1948	1952	1954*	
16 plots	*P. megacephala*	1420	—	1	− 1419
	O. smaragdina	871	—	658	− 213
	A. longipes	0	—	1564	+ 1564
	I. myrmecodiae	164	—	55	− 109
	Total ..	2455	—	2278	
5 plots	*P. megacephala*	115	0	0	− 115
	O. smaragdina	124	48	21	− 103
	A. longipes	0	249	294	+ 294
	I. myrmecodiae	111	41	9	− 102
	Total ..	350	338	324	

* A few of the figures in this column were actually obtained in early 1955.

In spite of these small discrepancies, however, the figures can be accepted as indicating the general trend in change of ant population. It will be seen from the available evidence that there appears to have been a succession of ant species as follows:—

Pheidole → *Oecophylla* → *Anoplolepis*

Whether the succession has in fact been as simple as this is by no means certain, and the possibility of further complications will be discussed later in the light of evidence from other areas.

The figures for *Iridomyrmex myrmecodiae* involve only one plot (TN) and very small parts of two others (KA and KE.2); although they indicate a very marked decrease, there is further evidence that this is exceptional and does not represent the history of *Iridomyrmex* in these plantations as a whole; this also will be discussed in detail later.

Faielau and Pepesala (Russell Islands).

One plot in each of these plantations was recorded by Leach and O'Connor in 1948. Since the change in ant population was of a similar nature, they can be considered together. Figures for Pepesala are available only for the years 1948 and 1954, but for Faielau they are available for 1952 also, so that an intermediate stage in the change can be seen. The history, as in the Kukum/Lunga/Tenaru group, is one of replacement of *Pheidole* by *Oecophylla* (Table II); there is no subsequent replacement of *Oecophylla* by *Anoplolepis*, since the latter ant was absent from the areas in question. In another part of Faielau plantation, however,

a major battle was observed to be in progress in September 1955 between *Oecophylla* and *Anoplolepis*, in which the latter appeared to be attacking and replacing the former.

The decrease in total numbers of palms recorded for Faielau and Pepesala is due to the same reasons as given before. It should be mentioned that in 1954 the small dark ant *Paratrechina vividula* (Nyl.), somewhat resembling *Pheidole megacephala*, was present on a few palms; some specimens collected by Phillips in

TABLE II.

Numbers of palms in which the crowns were occupied by *Pheidole* and *Oecophylla* in plots in the Russell Islands in 1948, 1952 and 1954.

	Species of ant	Number of palms occupied			Total gains (+) or losses (—)
		1948	1952	1954	
Pepesala ..	*P. megacephala*	30	—	0	— 30
	O. smaragdina	32	—	57	+ 25
	Total ..	62	—	57	
Faielau ..	*P. megacephala*	372	97	5	— 367
	O. smaragdina	70	340	413	+ 343
	Total ..	442	437	418	

1952 and labelled "Faielau *Pheidole*" also proved to be this species, so that it is possible that Leach's original "*Pheidole* palms" carried a mixed population, and that the battle for supremacy had not been entirely between *Oecophylla* and *Pheidole*.

Although there is no nutfall in the Russell Islands, this does not affect the study of changes in ant population, and these two plots are of particular interest from the point of view of the creeper theory, since creepers are virtually absent and one would therefore have expected the change to be in the opposite direction. This will be further discussed later.

Rua Vatu (Guadalcanal).

This plantation was not investigated in 1948, but Phillips (1956, p. 581) gives an outline of its history and condition in 1953. In pre-war days it had been dominated by *Oecophylla* and there were no signs of nutfall until 1937. From

TABLE III.

Numbers of palms occupied by different ant species in plots RC and RD (Rua Vatu, Guadalcanal) in June 1953 and November 1954.

Species of ant	Number of palms occupied		Gains (+) Losses (—)
	June 1953	Nov. 1954	
P. megacephala	83	0	— 83
O. smaragdina	45	106	+ 61
Other species	11	82	+ 71
No ants present	49	0	— 49
Total	188	188	

then onwards *Pheidole* seems to have got the upper hand, and in 1953 occupied most of the plantation, which was then suffering from heavy nutfall (see Phillips, 1956, fig. 2). Phillips recorded a number of plots in 1953, and then, by checking these at intervals during the next two or three years and by initiating new plots, the author was able to detect a most dramatic change in population in the reverse direction. Figures will be given for two instances, which typify the kind of change which was taking place during this period over all that part of the plantation previously occupied by *Pheidole*.

The first concerns two of Phillips's plots (RC and RD) which are adjacent and can be considered together (Table III). The second concerns a larger plot started in 1955 (Table IV). The general picture is the same as before, in that *Pheidole megacephala* was largely replaced by *Occophylla*. As in the Russell Islands, *Anoplolepis* does not appear in these plots. Certain other ants were involved in the change, however, referred to in the Tables as " other species ";

TABLE IV.

Numbers of palms occupied by different ant species in plot RJ. 1 (Rua Vatu) on different dates in 1955 and 1956.

Species of ant	Number of palms occupied				Total gains (+) or losses (−)
	August 1955	November 1955	March 1956	October 1956	
P. megacephala	207	183	1	0	− 207
O. smaragdina	7	16	55	88	+ 81
Other species	0	11	132	108	+ 108
No ants present	0	4	26	18	+ 18
Total	214	214	214	214	

these include the " minor species " referred to in Part I of this work; together with the absence of ants on some palms, they are of interest from the point of view of species replacement or succession. The changes in population at Rua Vatu were in fact somewhat complex, and varied in different parts of the plantation. They were studied in some detail and will be fully discussed later. The interesting thing to note here is that, for the majority of the plantation, the ultimate result at Rua Vatu is similar to that in the other examples given above. The accompanying change in the nutfall situation has already been discussed in Part I (Brown, 1959).

Lunga (Guadalcanal)—a return to Pheidole.

The examples of relatively rapid change in ant population given above all involve a replacement of *Pheidole* by beneficial ants, so that in those areas where there was nutfall at first, the change was accompanied by recovery from it. In the Kukum/Lunga/Tenaru group the changes resulted in such complete suppression of *Pheidole megacephala* that it appeared to have been wiped out altogether. It was therefore rather a surprise, in January 1955, to find one or two small areas in Lunga plantation where this ant had survived. One of these areas was on or near the site of Leach's plot LG, which had been a *Pheidole* area in 1948 but which had never been accurately identified since. In January 1955, *Pheidole* occupied an area of 3·16 acres, containing 97 palms of which two still retained *Occophylla* in the crowns and one was without any ants; a new plot (LQ) was made of this area. The surrounding area was occupied partly by *Occophylla* and partly by *Anoplolepis*. In February 1956, 13 months later, *Pheidole* had increased

its area to a total of 9·13 acres, containing 257 palms of which one still retained *Oecophylla* in the crown and 28 were without any ants. In November 1956, just over 10 months later, the *Pheidole* area had increased to 15·56 acres, containing 438 palms of which 16 still retained *Oecophylla* and two *Anoplolepis* in the crowns, and 49 were without any ants. Thus in a period of just over 21 months, the total area occupied by *Pheidole* had been increased by a factor of approximately five, and the number of palms it occupied by a factor of over four. These figures are set out in Table V; since the whole area involved was not plotted at the first recording, it is not possible to present complete figures as in the previous examples.

TABLE V.

Figures showing spread of *Pheidole megacephala* in plot LQ at Lunga (Guadalcanal).

Date	19.i.1955	24.ii.1956	1.xi.1956
Total area occupied (acres)	3·16	9·13	15·56
Palms occupied by :—			
P. megacephala	94	228	371
P. megacephala+*O. smaragdina*	2	1	16
P. megacephala+*A. longipes*	0	0	2
Palms without ants	1	28	49
Total palms	97	257	438

A similar change, although of a less spectacular nature, was observed in Leach's plot LF, also in Lunga plantation and not far from plot LQ. The original plot had been occupied almost entirely by *Pheidole*, but in 1954 this ant was confined to one palm and the trunk-bases of a few others; of the other palms, most were occupied by *Anoplolepis*, and a few by *Oecophylla*. From this date onwards *Pheidole* gradually spread and reoccupied many of the palms which it had lost. Its spread was steady (Table VI), accompanied first by an increase in

TABLE VI.

Figures showing spread of *Pheidole megacephala* in plot LF at Lunga (Guadalcanal).

Date	20.ix.54	14.v.55	21.ix.55	14.iii.56	26.ix.56	Over-all gains (+) or losses (—)
Palms occupied by :—						
P. megacephala	1	5	13	20	29	+28
P. megacephala+*O. smaragdina*	1	10	8	8	12	+11
P. megacephala+*A. longipes*	9	12	22	19	15	+ 6
O. smaragdina	8	3	1	0	0	— 8
A. longipes	55	46	32	28	19	— 36
O. smaragdina+*A. longipes*	2	0	0	0	0	— 2
Total palms ..	76	76	76	75	75	

the number of palms which it occupied jointly with either *Oecophylla* and *Anoplolepis*; the number of palms occupied exclusively by these latter ants showed a corresponding steady decrease.

Relatively stable Populations.

It will be noted that all the examples given above, of rapidly changing ant populations, involve *Pheidole megacephala*; also *Oecophylla* and sometimes *Anoplolepis* as well. Some examples will next be given of ant populations which, over the period of observation, have remained relatively stable.

Baunani (*Malaita*).

Two plots in this plantation can be quoted to illustrate stability.

One of these is a plot first recorded in May 1951 by O'Connor when he liberated the parasitic Tachinid fly, *Trichopoda pennipes* (F.), in an attempt to control *Amblypelta*, in a nutfall area dominated by *Iridomyrmex myrmecodiae*. The plot has since been re-checked three times over a period of four years (Table VII). The changes involved are insignificant compared with those in the examples given previously.

TABLE VII.

Numbers of palms occupied by different ant species in a plot in Baunani Plantation (Malaita) at different periods.

Species of ant	Number of palms occupied				Total gains (+) or losses (−)
	May 1951	February 1952	September 1954	May 1955	
I. myrmecodiae	97	95	88	87	− 10
O. smaragdina	11	12	14	14	+ 3
A. longipes	4	5	9	10	+ 6
Total	112	112	111	111	

The other Baunani plot (B.1) has been under observation for only a short period, but the numbers of palms and of species of ant involved are larger. The changes over the period of observation (Table VIII) are not very great by comparison with those in plots considered above.

TABLE VIII.

Numbers of palms occupied by different ant species in plot B.1 in Baunani Plantation (Malaita) on two different dates.

Species of ant	Number of palms occupied		Total gains (+) or losses (−)
	10.ix.1954	30.v.1955	
I. myrmecodiae	66	78	+12
A. longipes	86	87	+ 1
O. smaragdina	96	106	+10
P. megacephala	6	2	− 4
T. detorquens	22	29	+ 7
Other ants	15	13	− 2
No ants present	25	1	− 24
Total	316	316	

The Kukum/Lunga/Tenaru group of plantations.

Although the Kukum/Lunga/Tenaru group of plantations has been characterised on the whole by rapidly changing populations, there are areas within the group where there has been considerable stability. These mainly involve *Iridomyrmex myrmecodiae* as the principal ant, and, in considering illustrative examples, only the numbers of palms occupied by this ant will be taken into account.

The largest area of *Iridomyrmex* in these plantations is one of some 50 acres at Tenaru (plot TX). Phillips (1956, p. 580 and Table II) has described a somewhat spectacular reduction of *Iridomyrmex* in a small part (plot TN) of this area between 1948 and 1952, its place being taken by *Anoplolepis*. It seems that there was in fact, during that period, a fairly substantial retreat by *Iridomyrmex* at several points round the circumference of its area, but not by any means at all points, and since the whole area was not accurately plotted in 1948 it is difficult to obtain precise data. In 1954, however, conditions appeared to become stabilised, and the outline was accurately plotted palm by palm and re-checked at 6-monthly intervals until 1956. During this two-year period, out of an initial number of approximately 1,660 palms occupied by *Iridomyrmex*, a total of only 52 were 'lost' to *Anoplolepis* or other species of ants (an average of 1·6% per annum); this figure includes the off-setting of losses at some points by gains at others, but the over-all condition was one of stability.

The next largest *Iridomyrmex* area is plot KX at Kukum; in 1954, *Iridomyrmex* occupied 815 palms, and in 1956 this number had increased by only 15 (or 0·92% per annum).

Although two smaller *Iridomyrmex* areas (plots KA at Kukum and TP.2 at Tenaru) showed greater percentage changes during this period, the sum-total of all *Iridomyrmex*-occupied palms in all the four areas observed in this group of plantations, by a curious coincidence, remained exactly the same, as shown by the following summary:—

Plot	Initial number of palms with *Iridomyrmex*	Net gains (+) or losses (—) by *Iridomyrmex*
KA	22	+ 22
KX	815	+ 15
TP.2	57	+ 15
TX	1660	— 52
Total ..	2554	0

This suggests that areas occupied by *Iridomyrmex* tend to remain much more stable than those occupied by *Pheidole*; circumstantial, although less precise evidence from other areas supports this conclusion. It is not really surprising when one considers that *Iridomyrmex myrmecodiae* is an indigenous species, and is therefore more likely than the introduced *Pheidole megacephala* to maintain a condition of equilibrium with other species in its environment.

There is some evidence from one area (plot TO) at Tenaru, of a tendency towards stabilisation even in the absence of *Iridomyrmex*. The southern part of this plot was occupied entirely by *Anoplolepis* and *Oecophylla* (mainly the former) in 1954, and doubtless represented a late stage in the overrunning of an *Oecophylla* area by *Anoplolepis* which had been occurring nearly everywhere in this group of plantations. Re-checks in 1955 and 1956, however, showed that not only was this process coming to a halt, but that *Oecophylla* was even making some recovery and regaining part of its lost territory. The figures from counts in the three years (Table IX) illustrate this. The occurrence of many palms apparently without

TABLE IX.

Numbers of palms occupied by different ant species in plot TO at Tenaru (Guadalcanal), 1954–1956.

Dominant ants	Number of palms occupied			Total gains (+) or losses (−)
	August 1954	March 1955	August 1956	
A. longipes	973	1001	907	− 66
O. smaragdina	97	87	141	+44
A. longipes + *O. smaragdina* ..	95	69	29	− 66
Other species	—	—	10	+10
No ants present	—	—	63	+63
Total	1165	1157	1150	− 15

The decrease in total number of palms is due to some falling as the result of war damage.

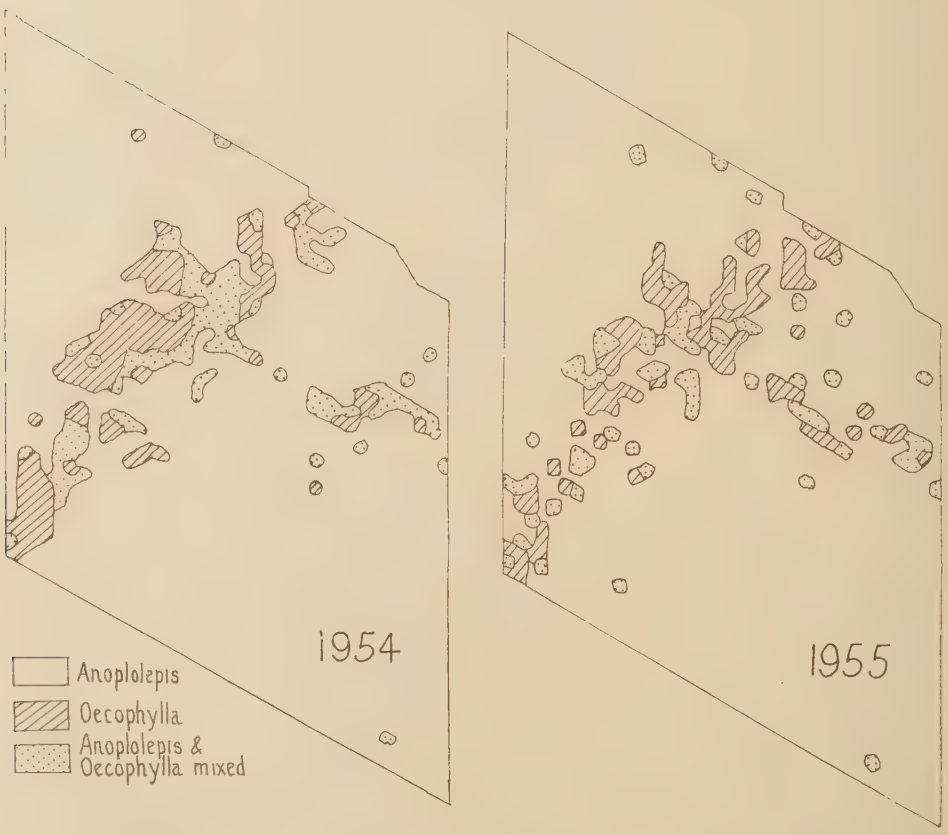


Fig. 1.—Part of plot TO at Tenaru, Guadalcanal, an area occupied by *Oecophylla smaragdina* and *Anoplolepis longipes*; the typical patchy distribution of *Oecophylla* in an area with *Anoplolepis* predominating, and the changes occurring between 1954 and 1955, should be noted.

ants in 1956 suggests a check in the spread of *Anoplolepis* due to intrinsic factors rather than to antagonism by *Oecophylla*.

There was evidence that a similar state of ' equilibrium ' between these two species, with *Anoplolepis* predominating, had been reached at this time in other parts of the Kukum/Lunga/Tenaru group of plantations. The form of distribution in such a mixed population of the two species is rather characteristic, with ' islands ' of *Oecophylla* of varying size scattered throughout a background of *Anoplolepis* (fig. 1), and a high proportion of palms carrying both species (*Oecophylla* in the crown and *Anoplolepis* at the base of the trunk). It is probable that many of these islands represent single monogynous colonies of *Oecophylla*, according to researches in Zanzibar by Way (1954, pp. 100 *et seq.*). There is a continual state of flux in the detailed distribution, individual palms or groups being lost and recaptured. The condition in plot TO at two periods separated by about seven months is illustrated in fig. 1.

The usual form of distribution for an *Iridomyrmex* colony is quite different (fig. 2); it generally forms a solid block, with the outline more clearly defined and with few palms carrying mixed populations. This appears to be due to three reasons: (i) the fact that *Iridomyrmex* forms immense, continuous polygynous colonies; (ii) a stronger mutual intolerance between it and other ants; (iii) in the case of contact with *Oecophylla*, the fact that both species inhabit mainly the crowns of the palms.

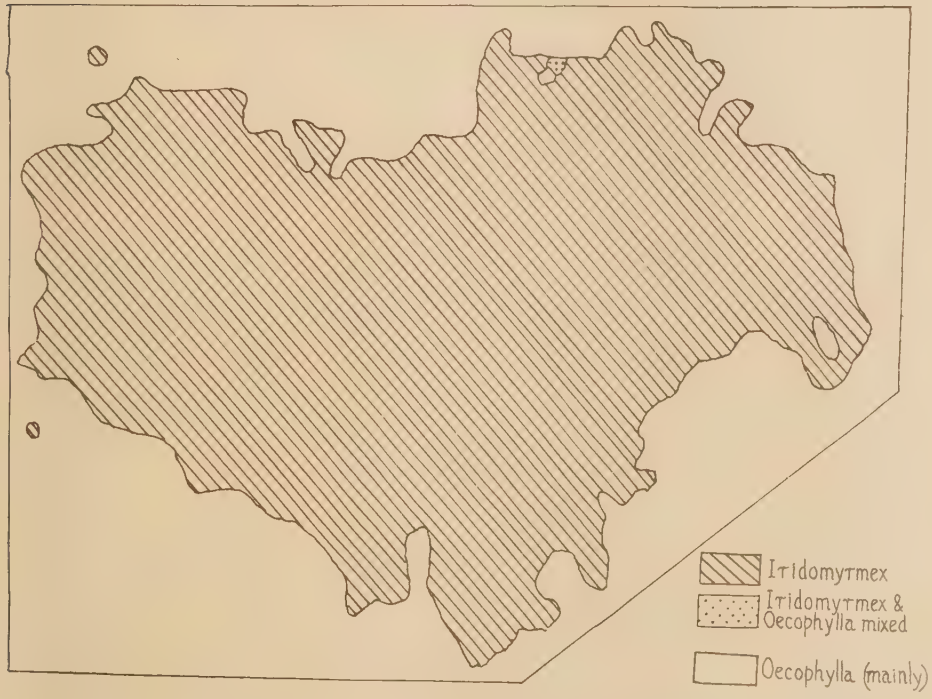


Fig. 2.—Plot KX at Kukum, an area occupied mainly by *Iridomyrmex myrmecodiae* and *Oecophylla smaragdina*; the tendency of *Iridomyrmex* to occupy a solid block of territory should be noted (compare the distribution of *Oecophylla* in fig. 1).

Ant Battles.

The process of replacement of one major species by another usually involves more or less serious fighting; this has been witnessed on several occasions, and some illustrative instances will be described. In general, the invading species advances from the ground on to the base of the trunk, where it attempts to build up its numbers. The ants of the species already in occupation then descend in force from the crown and form defensive lines, facing downwards, just above the base of the trunk. There is a zone of neutral territory (' no-man's land '), often only a few inches across, in between the two species; single ants venturing across this into the territory of the other species are usually quickly surrounded by several antagonists and overpowered. Gradually, through superior numbers, one or the other species makes headway into the territory of the other and drives it back.

(*a*) Pheidole *invading* Oecophylla.

A good instance of this was witnessed at Lunga (p. 528). *Pheidole megacephala* was advancing rapidly into *Oecophylla* territory, and at the periphery of its area of spread its ' advanced guard ' was installed on the bases of the trunks of a number of palms which still had *Oecophylla* colonies in the crowns. On the bases of the trunks of many of the palms were some old earthen runways of termites, and *Pheidole*, being small, had concealed itself in these; where there were small holes in the wall of the runway, *Pheidole* were stationed with heads facing outwards. Meanwhile large numbers of *Oecophylla* had descended from the crown on to the base of the trunk within an inch of the *Pheidole* position, and there was, more or less, a state of deadlock (Pl. XII, fig. 1); the *Oecophylla* ants were unable to get access to the *Pheidole*, while the latter were in insufficient numbers to attack. When an individual of *Pheidole* ventured out of its shelter it was immediately set upon by a number of *Oecophylla* and killed. On one palm this state of tension was observed first on 10th October, and the position was apparently still unchanged at the time of the last observation on 18th November. That most of such battles eventually turned in favour of *Pheidole* is evident from the rapid territorial advances it was making at this period.

(*b*) Anoplolepis *invading* Iridomyrmex myrmecodiae.

A battle between these two species at the margin of the large *Iridomyrmex* area at Tenaru (p. 531) took somewhat the same form as the above. *Anoplolepis* had advanced on to the base of the trunk of a palm occupied by *Iridomyrmex*, which had descended in force from the trunk and formed a formidable phalanx of countless individuals, almost completely covering the surface of the trunk over about 2 ft. of its length. After a few days this defensive formation was still intact, but had retreated higher up the trunk; eventually it was driven from the trunk altogether, and later *Anoplolepis* took possession of the crown. The latter part of the invasion was not observed in detail.

(*c*) Anoplolepis *invading* Oecophylla.

These are the species which have been most frequently observed in conflict (*e.g.*, at Kukum, Tenaru, in the Russell Islands and elsewhere). As in the other cases, the invading *Anoplolepis* ants move on to the base of the trunk, which evokes the descent of large numbers of *Oecophylla* to ring the trunk in defensive formation just above them. It then becomes a ding-dong struggle, the dividing line between the two species sometimes moving up or down a few feet from day to day; any ant wandering alone into the other species' territory is usually surrounded and overcome. Eventually one species will get the better of the other, but this may not happen for several days or even weeks.

All the instances described above take the same general form—invasion of a

predominantly arboreal, tree-nesting species (*Occophylla* or *Iridomyrmex*) by a predominantly ground-nesting species (*Anoplolepis*) or one which is at least equally at home at ground level as in the crown (*Pheidole megacephala*); the attack starts at the base of the trunk and works upwards, the final deciding factor depending only, as far as one can see, upon the relative strength (in terms of numbers) of the two species. Downward invasion by an arboreal species of a ground species must sometimes occur in a somewhat similar manner, although the details were never actually observed.

Types of Vegetation associated with Ant Species.

There is, under present conditions, a considerable variety of vegetation in the coconut plantations of the Solomon Islands. This is mainly, but not entirely, due to neglect during the war years, when natural vegetation, including trees and many kinds of creepers, got out of control and invaded the plantations. These plants include some introduced and semi-cultivated species (*e.g.*, leguminous cover crops) but are mainly wild species. In several plantations, especially in those of the Western Islands where post-war rehabilitation has been negligible, the trees have attained or even surpassed in height that of the palms, and the condition somewhat resembles that of tropical forest. In such cases there is more scope for variety in types of vegetation. Both wild creepers (Pl. XVI, fig. 2) and cultivated species (Pl. XV, fig. 3) have overgrown the palms, and their wiry stems have formed dense tangles on the trunks (Pl. XII, fig. 3). Trees are of many species, and perhaps the most important are several species of *Ficus*, some of which (Pl. XIII, fig. 2) are epiphytic on the coconut palms. In the few plantations, on the other hand, which have remained well-tended throughout, or which were rehabilitated early after the war (Pl. XIV, fig. 4), conditions are naturally more homogeneous, since vegetation has been kept short and the growth of trees and shrubs discouraged; this has sometimes been brought about by weeding or ' brushing ', and sometimes by cattle, but the latter were destroyed during the war except on a few plantations such as Pepesala (Pl. XIV, fig. 4).

List of prevalent Plants.

It will assist the reader if some of the more important or conspicuous plants found in the plantations are listed. They will be grouped according to habit of growth (trees and shrubs, herbaceous plants, creepers and climbers, and epiphytes) and by families.

(*a*) *Trees and shrubs.*

These two categories are considered together, because many species normally growing to the height of trees have only had time to reach shrub size in the plantations.

Casuarinaceae: *Casuarina* sp. Combretaceae: *Terminalia* sp. Euphorbiaceae: *Breynia cernua* Muell. Arg.; *Homalanthus populneus* (Giesel.) Pax.; *Macaranga tanarius* (L.) Muell. Arg.; *Macaranga* is extremely common, often of the size of a shrub rather than a tree. Guttiferae: *Calophyllum* sp. Lecythidaceae: *Barringtonia* sp. Leguminosae: *Cassia alata* L.; *Tephrosia* sp. Malvaceae: *Hibiscus tiliaceus* L. Moraceae: *Ficus* spp. form an important element in the vegetation. Several species were identified from coconut plantations, and they may be divided into two groups ecologically: free-living forms, of which *F. septica* Rumph. and *F. copiosa* Steud. are the most abundant, and which include also *F. chaetophora* Warb., *F. wassa* Roxb., and *F. ? bernaysii* King (or a closely related species), and *F. frondosa* S. Moore; and epiphytic forms which may

actually grow on the coconut palms and strangle them in the later stages, of which *F. tinctoria* Forst. f. (Pl. XIII, fig. 2) and *F. benjamina* L. are the most abundant, and which include also *F. prolixa* Forst. f., *F. subulata* Bl. and *F. ? distichoidea* Diels.; the last two species are climbers rather than epiphytes; although the epiphytic and climbing species should be treated under other appropriate headings, all *Ficus* spp. are considered together here for convenience, and because they mostly assume the form of trees in their ultimate development. Apart from the strangulation effect of the epiphytic species, which has no bearing upon nutfall, several species, both free-living and epiphytic, may be of importance in areas occupied by *Oecophylla*, which shows a preference for these trees for nesting purposes; this will be further discussed later. Myrsinaceae: *Maesa* sp. Myrtaceae: *Psidium guajava* L. Pandanaceae: *Pandanus* spp. Rubiaceae: *Morinda citrifolia* L.; *Timonius* sp.; the latter (locally known as 'sarkosié') is a tree very characteristic of poor soils. Rutaceae: *Citrus* sp.; most of the *Citrus* scattered through the plantations are 'bush limes'; they are of importance for *Oecophylla* for the same reasons as *Ficus* spp. (see above); *Evodia* sp. Sapindaceae: *Cupaniopsis* sp. Scitamineae (= Zingiberaceae): 'wild gingers' are extremely abundant, and owing to their powers of rapid regeneration frequently dominate the vegetation of plantations which have been untended for a year or more; a red-flowered species of *Curcuma* and a white-flowered *Alpinia* are the most widespread and abundant; their ecological importance is problematical, and will be discussed in connection with *Oecophylla*. Urticaceae: *Pipturus* sp. aff. *incanus* Wedd. Verbenaceae: *Vitex negundo* L.

(*b*) *Herbaceous plants.*

A very large number of small, low plants could be listed, but since they are mainly of little or no importance, only some of the commonest will be mentioned here.

Araceae: *Alocasia* sp.; 'wild taro' is common and widespread. Asclepiadaceae: *Asclepias curassavica* L. Commelinaceae: *Commelina benghalensis* L.; *C. diffusa* Burm. f.; *Pollia macrophylla* (R. Br.) Benth. Compositae: *Ageratum conyzoides* L.; *Bidens pilosa* L.; *Bidens* sp.; *Eleutheranthera ruderalis* Sch. Bip.; *Synedrella nodiflora* (L.) Gaertn. Convolvulaceae: *Ipomoea pes-caprae* (L.) R. Br., the 'beach morning glory', is often a dominant ground plant in those parts of plantations nearest to the sea. Euphorbiaceae: *Euphorbia hirta* L. Gramineae: a fairly large number of grasses are found, although they are seldom dominant and are usually mixed with other plants; the following are among the more prevalent ones:— *Axonopus affinis* Chase; *Centotheca lappacea* (L.) Desv.; *Chrysopogon aciculatus* (Retz.) Trin.; *Cyrtococcum patens* (L.) A. Camus; *Eleusine indica* (L.) Gaertn.; *Imperata exaltata* (Roxb.) Brongn.; *Ischaemum muticum* L.; *Oplismenus compositus* (L.) Beauv.; *Paspalum conjugatum* Berg. Leguminosae: *Canavalia turgida* Grah. and other species (often near the sea and mixed with *Ipomoea pes-caprae*); *Crotalaria* spp.; *Derris trifoliata* Lour. (especially in damp soils); *Desmodium* spp. (including *canum* (Gmel.) Schinz. & Thell., *heterophyllum* DC., *ormocarpoides* DC., *siliquosum* (Burm. f.) DC., *triflorum* (L.) DC., *zonatum* Miq.); *Mimosa pudica* L. (a very troublesome weed locally); *Mimosa invisa* Mart.; *Vigna marina* (Burm.) Merr. Malvaceae: *Sida acuta* Burm. f.; *S. rhombifolia* L.; *Urena lobata* L. Passifloraceae: *Passiflora foetida* L. Polygalaceae: *Polygala paniculata* L. Polypodiaceae: ferns are widespread in plantations, and one or other of two species (*Dryopteris unita* (L.) O. Kuntze and *Nephrolepis hirsutula* (Forst.) Presl.) is frequently the dominant herbaceous plant; other common species in plantations are the edible *Diplazium esculentum* (Retz.) Sw., and *Polypodium* spp. Rubiaceae: *Borreria* sp. Selaginellaceae: *Selaginella rechingeri* Hieron, and other spp. less frequently.

SOLANACEAE: *Solanum ficifolium* (Ortega), the 'devil's fig' (commonly but incorrectly called *Solanum torvum*) is very local, but may grow into a woody plant several feet high and then becomes a serious weed; it should then be more correctly included among 'shrubs'. TILIACEAE: *Triumfetta procumbens* J. R. & G. Forst.; *T. rhomboidea* Jacq. URTICACEAE: *Boehmeria* sp. VERBENACEAE: *Stachytarpheta dichotoma* Vahl.; *S. jamaicensis* (L.) Vahl., var. *indica* (L.) H. J. Lam.

(*c*) *Creepers and climbers.*

Creepers and climbers, together with epiphytes, are ecologically the most important plants from the point of view of the nutfall problem, since they have been considered as influencing the ant population of the palms up which they climb; a more complete list of those observed is therefore given. It is occasionally not easy at once to distinguish a creeper from an epiphyte, since some kinds of the latter may creep up stems and have the same habit of growth, although capable of surviving even after being severed from the ground (*e.g.*, the fern *Pyrrosia acrostichoides* (Forst.) Ching). There are some plants which have not been put to such a test, and the following lists are therefore arbitrary as far as these are concerned; this, however, is of no great importance for present purposes. ARACEAE: *Epipremnum pinnatum* (L.) Engl.; this is a very conspicuous and widespread creeper with large, smooth leaves (Pl. XII, figs. 2, 3). ASCLEPIADACEAE: *Dischidia* is an important genus in connection with the ant, *Iridomyrmex myrmecodiae*; *D. milnei* Hemsl., with circular leaves (Pl. XIV, fig. 1) is the most interesting; *D. cominsii* Hemsl., with very small leaves and forming a dense growth on the trunk, is less widespread; *Hoya schneei* Schltr. is another common species. COMPOSITAE: *Mikania scandens* L., an introduced plant, is frequent on coconut palms. CONVOLVULACEAE: *Ipomoea congesta* R. Br. ('blue morning glory') is an abundant trailing ground plant, which climbs the trunks of coconut palms and other supports which present themselves. LEGUMINOSAE: all the following are important trailing plants, but will ascend coconut trunks to varying heights; *Derris trifoliata* Lour., *Desmodium* spp. and *Vigna marina* (Burm.) Merr. rarely ascend more than 2–3 ft., but *Calopogonium mucunoides* Desv., *Centrosema* sp., and *Pueraria* spp. (mostly *P. phaseoloides* Benth. and *P.* sp. aff. *psoraleoides* Benth.) will ascend higher, even up into the crowns of the palms (Pl. XV, fig. 3). MENISPERMACEAE: *Stephania* sp. aff. *forsteri* (DC.) A. Gray. PASSIFLORACEAE: the tropicopolitan *Passiflora foetida* L. PIPERACEAE: the genus *Piper* is one of the most important in the composition of the climbing flora of the palm trunks (Pl. XIII, fig. 3); several species occur commonly, but the genus is in need of revision and no specific names can be given. POLYPODIACEAE: of the climbing ferns, two species are of special importance: *Stenochlaena juglandifolia* Presl., which may form dense growths ascending to the crowns of the palms (Pl. XVI, fig. 2), and *Polypodium sinuosum* Wall., which has hollow stems and is especially associated with *Iridomyrmex myrmecodiae*. SCHIZAEACEAE: this is another family of ferns containing the genus *Lygodium*, of which three species (*circinnatum* (Burm.) Sw., *microphyllum* (Cav.) R. Br., and *trifurcatum* Bak.) frequently ascend the bases of coconut palms.

(*d*) *Epiphytes.*

Epiphytes are plants which can live on the surface of the palm trunks without the necessity of contact with the ground; the species are fewer, but include both flowering plants and ferns.

ORCHIDACEAE: a large number of species of orchids grow on the trunks: *Grammatophyllum* sp. (Pl. XIII, fig. 4) is fairly typical, but there is a very wide range in habit of growth. POLYPODIACEAE: *Asplenium nidus* L., *Merinthosorus drynarioides*

(Hook.) Copel. and *Polypodium* spp. form usually localised growths, while *Pyrrosia acrostichoides* (Forst.) Ching has more the habit of a climbing plant. RUBIACEAE: *Hydnophytum formicarium* Jack. (Pl. XIV, fig. 3) and *Myrmecodia* sp. *cf. solomonensis* Becc. (Pl. XIV, fig. 2) are two interesting and common species associated especially with *Iridomyrmex myrmecodiae*, in connection with which they will be discussed further.

Vegetation associated with *Oecophylla smaragdina.*

The main interest of the vegetation of areas dominated by *Oecophylla* is in relation to the creeper theory (p. 524). If this theory is correct, we should find *Oecophylla* predominating mostly in areas with creepers climbing up the trunks, or in which such creepers have been present until recently. This is not found to be the case. On Plate XIV (fig. 4) is shown an area of Pepesala plantation, in which *Oecophylla* was dominant; it is free from excessive vegetation of any kind, and especially from creepers; illustrations of several other similar areas could be given, *e.g.*, Buma on Malaita and Pawa on Ugi (San Cristobal). Several such areas have been maintained in a similar condition over a period of at least several years, and in two at least (Pawa and Pepesala), *Pheidole megacephala* has been present in recent years and was still present in small numbers at Pawa when it was examined in 1955. It seems, therefore, that *Oecophylla* has not only maintained its status but even extended its range, in competition with *Pheidole*, while such conditions prevailed. Several other very similar, creeperless localities have been discovered in which *Oecophylla* was dominant; out of a total of 19 plots and samples, 11 were almost or entirely free from creepers on the trunks, in four they were rare and could not have been of any major ecological significance, and only in the remaining four were they at all common (mainly *Epipremnum pinnatum*, *Piper*, *Lygodium* and, once each, *Stenochlaena juglandifolia* and *Pueraria phaseoloides*).

Epiphytes are, about equally with creepers, of very minor frequency in most *Oecophylla* areas.

If any one species of creeper is more closely associated with *Oecophylla* than others it is the Aroid *Epipremnum pinnatum* (Pl. XII, fig. 2), and the connection may be related to the large Margarodid mealybug, *Steatococcus samaraius* Morr., which occurs especially on this plant and which is tended assiduously by *Oecophylla.*

Another plant which, although not a creeper, could perform the functions of one from the point of view of the creeper theory, is wild ginger (*Curcuma* and *Alpinia*). These plants may form a continuous, dense growth over large areas, and their tall, flexible stems often contact the trunks of the palms and form a bridge by which *Oecophylla* can cross from one palm to another without touching the ground (Pl. XII, fig. 4). *Oecophylla* has been actually observed to do this, but whether it has any important effect on its spread is another matter, and will be further discussed later.

Of other plants, there are two trees which are often associated with *Oecophylla*, namely *Ficus septica* and *Citrus*; they are nearly always frequented by large numbers of the ant, which makes its nests in them and tends certain Coccids which are found on them, especially *Coccus mangiferae* (Green), *Laingiococcus painei* (Laing) and *Saissetia nigra* (Nietn.) on *Ficus*, and *Coccus hesperidum* L. on *Citrus*. *Breynia cernua* is another such shrub, but is less widespread and the evidence therefore less strong. It is possible that the encouragement of these trees in plantations already partly occupied by *Oecophylla* would assist its spread, but this has not yet been put to a thorough test. Certain epiphytic species of *Ficus* are also related ecologically to *Oecophylla* in a similar manner (*e.g.*, *F. tinctoria* and *F. benjamina*), but since they are harmful to coconut palms it is obviously not practical to encourage them.

Vegetation associated with *Anoplolepis longipes.*

There is little fundamental difference between the vegetation of *Anoplolepis* and *Oecophylla* areas; in several cases the two are identical, the same area being partly dominated by *Oecophylla* and partly by *Anoplolepis*. However, there is a tendency for the latter to be commoner in more overgrown areas. Out of 15 areas in which it was dominant, four were very overgrown with abundance of creepers, four moderately so, and three with fewer creepers; only four were almost or entirely free from creeper growth, and, of these, two had been recently 'brushed'. There is no obvious reason for this, except that *Anoplolepis* tends to run under creepers while *Oecophylla* runs on the outside of them, so that, when these two ants are in competition, *Anoplolepis* may have the advantage of protection where creepers are present. Since both of these ants are beneficial as far as nutfall is concerned, this is not important economically. .

The creepers most frequently present were *Ipomoea congesta*, *Pueraria psoraleoides*, *Calopogonium mucunoides* (Pl. XV, fig. 1), *Centrosema*, *Epipremnum pinnatum*, *Piper*, and *Lygodium circinnatum*, with *Passiflora foetida* and *Mikania scandens* also occurring more rarely.

Epiphytes are apparently of no importance; orchids were found occasionally, and the ferns, *Pyrrosia acrostichoides*, *Asplenium nidus*, *Merinthosorus drynariodes* and *Polypodium* sp.

Trees, shrubs and herbaceous plants were very numerous in species and not obviously differing from those in *Oecophylla* areas. Ground vegetation can be either sparse or thick. Since *Anoplolepis* does not tend Coccids, there was no association, as in *Oecophylla*, with particular plants in connection with these insects. *Anoplolepis*, however, is a sugar feeder, and an association was frequently noticed between it and certain leguminous plants with extra-floral nectaries. The chief of these are *Cassia alata*, *Crotalaria mucronata* Desv., *Pueraria phaseoloides*, *Pueraria psoraleoides* and *Calopogonium mucunoides*. The nectaries of *Cassia* are at the base of the petioles (Pl. XV, fig. 2), and those of the other genera are in the inflorescences at the bases of the pedicels. Although *Anoplolepis* feeds assiduously at the nectaries, there is not enough evidence to state definitely that the presence or absence of these leguminous plants acts as an important ecological factor in distribution. Since *Pueraria* and *Calopogonium* are useful cover crops, it would be worth trying to establish them on an experimental scale in suitable areas, to find out how much influence they have.

Vegetation associated with *Pheidole megacephala.*

Fewer areas were found with *Pheidole* dominant, so that there is less evidence on which to form judgment regarding the characteristic vegetation. Creepers are of frequent occurrence and the palm trunks are often very overgrown. Of ten areas with *Pheidole* dominant and in very large numbers, three had a very dense growth of creepers, four were very overgrown generally with creepers abundant but less dense, and three had very few creepers (Pl. XV, fig. 4). In one (similar to Pl. XVI, fig. 2) the climbing fern, *Stenochlaena juglandifolia*, was the principal creeper; in others there were mixtures of *Pueraria* and *Centrosema* (Pl. XV, fig. 3) or of *Pueraria*, *Piper*, *Stenochlaena* and *Epipremnum*; occasionally, also, *Lygodium*, *Stephania*, *Vigna marina*, and *Ipomoea congesta* occurred. In general, the incidence of creepers was far higher than in areas dominated by *Oecophylla*. This is completely contrary to what one would expect on the basis of the creeper theory. The creepers, as opposed to assisting the spread of *Oecophylla*, seem to favour *Pheidole*, and this they appear to do by providing a protected route up and down the trunk; *Pheidole* utilises the spaces between the massed creeper stems encrusting the trunk, and also any disused termite runways there may be, for covered runways (Pl. XII, fig. 1; Pl. XVI, fig. 1). To this extent, creepers may

be regarded as beneficial to *Pheidole*; at the same time, they do not appear to be a necessity, because *Pheidole* can be dominant in areas without creepers, and at Lunga was actually extending its range rapidly in an area with very few creepers (Pl. XV, fig. 4).

Epiphytes were scarce in *Pheidole* areas, only *Pyrrosia acrostichoides* being at all common.

Other common plants included wild gingers (*Alpinia* and *Curcuma*, which on several occasions formed a very dense undergrowth), *Ficus* spp. (both epiphytic and free-living), and the ferns, *Nephrolepis hirsutula* and *Dryopteris unita*. The plants associated with *Pheidole* by Leach (*in* O'Connor, 1950), namely *Paspalum*, *Mimosa pudica* and *Triumfetta*, were not recorded, and certainly could not have been conspicuously common, in *Pheidole* areas in the present work.

Although *Pheidole* tends mealybugs, the species with which it is mainly concerned are associated with the coconut palm itself, so that other plants do not appear to have any important influence from this point of view.

Vegetation associated with *Iridomyrmex myrmecodiae*.

Above all other species, *Iridomyrmex* tends to have definite associations with certain kinds of plants; so much so that it is often possible to recognise an *Iridomyrmex* area on sight, which cannot be said of any of the other species of ants.

The most characteristic flora for an *Iridomyrmex* area is one in which epiphytic plants predominate. These include the ferns, *Pyrrosia acrostichoides* (Pl. XIII, fig. 3) and *Asplenium nidus*, several species of orchids (Pl. XIII, fig. 4), and (especially characteristic and in the writer's experience almost entirely confined to *Iridomyrmex* areas) the Rubiaceous species *Myrmecodia* sp., *cf. solomonensis* (Pl. XIV, fig. 2) and *Hydnophytum formicarium* (Pl. XIV, fig. 3). These last two plants have a swollen tuberous base to the stem, which, when cut open, reveals an internal labyrinth of interconnecting cavities, in which *Iridomyrmex* swarms in enormous numbers. These epiphytes form tufted growths on the trunks, unconnected with the ground, giving a characteristic appearance to the palms (Pl. XVI, fig. 3).

In addition to epiphytes, there are several species of creepers, some of which are characteristic of *Iridomyrmex* areas and may be partly epiphytic in habit. Of these, the Asclepiad genus, *Dischidia*, is important; one species, *Dischidia milnei*, has circular leaves with the underside convex, and the surrounding margins closely appressed on to the surface of the trunk, so that there is a space beneath each leaf (Pl. XIV, fig. 1), which is also inhabited by the ants; another species, *Dischidia cominsii* has no such specialisation of the leaves, but the stems and leaves together form a matted growth on the trunk which provides shelter; the same is the case with the related *Hoya schneei*. A fern, *Polypodium sinuosum*, has dilated stems with a cavity running up the centre, which *Iridomyrmex* (and very occasionally other ants) use as runways.

In addition to the above plants, which are specially associated with *Iridomyrmex*, several other creepers occur abundantly with this ant, without being in any way limited to areas occupied by it, since they may be associated equally with *Pheidole*; such are *Stenochlaena juglandifolia* (Pl. XVI, fig. 2) and *Calopogonium*, *Epipremnum pinnatum*, *Piper*, etc.

Two examples will serve to emphasise the close connection of *Iridomyrmex*, by contrast with *Oecophylla* and *Anoplolepis*, with epiphytes and creepers. In Kau-Kau plantation on Guadalcanal there were adjacent *Iridomyrmex* and *Oecophylla* areas, with a sharply demarcated dividing line between them. On a random sample of 60 palms on either side of the line, plants of different kinds were found on the numbers of palms shown below:—

	Iridomyrmex	*Oecophylla*
Creepers :		
Hoya schneei	26	3
Epipremnum pinnatum	1	0
Stenochlaena juglandifolia	1	0
Polypodium sinuosum	1	0
Epiphytes :		
Pyrrosia acrostichoides	16	4
Orchids :	37	30
Myrmecodia and *Hydnophytum* ..	43	0
Polypodium sp.	3	2
Total	128	39

The close correlation of *Iridomyrmex* with the creeper, *Hoya*, and the epiphytes, *Myrmecodia* and *Hydnophytum*, is very marked, and the trunks bearing vegetation distinguish the *Iridomyrmex* area very sharply from the bare trunks of the *Oecophylla* area (Pl. XVI, fig. 3); most of the vegetation on *Oecophylla* palms is accounted for by small orchid plants, which show less close correlation in general with any one species of ant.

The second example involves *Iridomyrmex* and *Anoplolepis* found in a patchwork distribution in an area of Baunani plantation on Malaita; in this case creepers (mostly *Stenochlaena juglandifolia*) were alone involved, and occurred on the following number of palms:—

	Iridomyrmex	*Anoplolepis*
Creepers present	62	1
Creepers absent	25	56

Two further examples illustrate the close association of *Iridomyrmex* with certain individual plant species. One concerns the fern, *Polypodium sinuosum*, in an area at Auki (Malaita); on a random sample of palms with and without this plant on the trunks, ants were distributed as follows:—

	Iridomyrmex	*Technomyrmex detorquens* (Wlk.)
Polypodium present ..	15	0
Polypodium absent ..	9	8

The other shows an even more marked association of *Iridomyrmex* with *Dischidia milnei* in Maru plantation (San Cristobal):—

	Iridomyrmex	Other spp. of ant	No ants present
Dischidia present ..	13	1	2
Dischidia absent ..	0	22	1

The "other species" of ant here included *Pheidole megacephala*, *Oecophylla smaragdina*, *Anoplolepis longipes*, *Odontomachus haematodes* (L.), *Camponotus irritans* (F. Sm.) and *Paratrechina* sp.

Iridomyrmex almost invariably has covered runways, and where plants do not provide complete cover, it usually fills in the gaps by constructing a roof of material looking like earth but consisting largely of vegetable matter (Pl. XIV, fig. 1).

Although plants, either epiphytes or creepers, or both together, are nearly always plentiful on the trunks, they are not essential, and *Iridomyrmex* can occur with little vegetation or even with none at all on the trunks; it then has to construct more extensive 'earthen' runways, and the trunk becomes merely the connecting route between its strongholds on the ground and those in the palm crowns; it can even extend its range in a plantation under these conditions (Pl. XVI, fig. 4).

The significance of the usual association between *Iridomyrmex* and epiphytes therefore becomes somewhat problematical. They are not essential to it, and yet when present they confer an obvious advantage on it, and in some cases show structural peculiarities which appear to be designed to give protective sanctuary to it. On the other hand, certain of these epiphytes (in particular *Myrmecodia* and *Hydnophytum*) rarely occur without *Iridomyrmex*, which suggests that their distribution is dependent on that of the ant rather than the latter's upon theirs. The explanation of this may be that the 'earthen' runways of the ant provide a medium in which the plants can more readily become established and grow; once established, the construction of further runways round their roots and stems provides more nourishment so that they grow larger and more extensive. If this is the case, *Iridomyrmex* areas at first without epiphytes may be expected to acquire them later. There are occasional areas in which there is a rich growth of epiphytes, but *Iridomyrmex* is absent; in such cases, however, *Iridomyrmex* is always present in an adjacent area, and it is probable that it was driven out by another species after the plants had become established; even epiphytes, therefore, do not entirely safeguard *Iridomyrmex* in the face of invasion by other species of ant.

Of 23 *Iridomyrmex* areas, two had epiphytes only on the trunks, and three creepers only; 16 had epiphytes with a variable proportion of creepers as well, and in only two were both epiphytes and creepers so scarce as to be negligible.

There is nothing remarkable about the trees, shrubs and herbaceous ground vegetation of *Iridomyrmex* areas. Like *Pheidole*, *Iridomyrmex* tends Coccids, but these are mostly attached to the coconut palm; several species have been found on other plants, however, such as *Coccus hesperidum* on *Barringtonia*, *C. viridis* (Green), *C. elongatus* (Sign.), *C. mangiferae*, *Saissetia nigra*, *S. oleae* (Bern.) and *Planococcus citri* (Risso) on *Wedelia biflora*, *Pseudococcus adonidum* (L.) and *P. leveri* Green and *C. mangiferae* on *Ficus septica*, and *Saissetia* spp. on *Sida rhombifolia*, and *C. mangiferae* on *Epipremnum pinnatum*. *Iridomyrmex* always constructs 'earthen' shelters over colonies of these Coccids, similar to those over its runways and often incorporated in them.

To summarise, we may conclude that of the four principal species of ants, only *Iridomyrmex myrmecodiae* shows a clear association with definite types of vegetation, and even here the association is not found invariably, and furthermore, much of this associated vegetation is probably the result of the presence of the ant rather than the cause of it. Of the other species, *Pheidole megacephala* tends to be associated more often with heavy creeper growth, but again the association is not invariable. *Anoplolepis longipes* and *Oecophylla smaragdina* show the least correlation with vegetation, but the latter tends to be dominant more often in open plantations with little creeper growth.

Vegetation associated with mixed Ant Populations.

We have dealt so far with areas in which one species of ant is clearly dominant over others. There are many plantations or parts of plantations, however, in which there is a mixture of species, including many indigenous species of minor importance from the point of view of nutfall, and which will be further discussed later.

Without going into details, it may be stated that, on the whole, mixed populations tend to occur in plantations which are very overgrown with creepers, wild trees and shrubs and other plants; in short, the more mixed the vegetation, the more varied the ant population. Out of 57 such mixed ant populations, from widely scattered localities, for which records were made, 22 were from very heavily overgrown areas, and 16 from areas with more than average amount of creepers and other vegetation; nine areas had a moderate amount, and only ten had very little. This is to be expected, since the encroachment of wild vegetation will create not only a return towards conditions more natural to the islands, but also greater ecological variety in the habitat, so that indigenous species of ants will more readily gain a footing than they would in the more homogeneous and less natural conditions of a well maintained plantation.

These mixed ant populations were found more especially in the Western Islands, where there had been less rehabilitation since the war years, and more of the plantations had remained in an overgrown condition.

It is interesting to speculate on the most probable effect on ant populations, on the evidence given above, of allowing creepers and undergrowth to develop on the one hand, or of keeping the plantations well weeded and in good condition on the other. The former policy would be likely eventually to encourage a mixed ant population, or if one of the major species became dominant it would be more likely to be *Pheidole* or *Iridomyrmex* than it would *Occophylla* or *Anoplolepis*. Good maintenance, on the other hand, would result in a nearer approach to an unnatural, monospecific population, and symptoms of nutfall would become more definitely positive or negative according to which species acquired dominance. There is no conclusive evidence that this species would be either a beneficial or a harmful one; but the fact that *Occophylla* is more frequently dominant than any other in the better maintained plantations suggests that the commonly held view that encouraging creepers also encourages *Occophylla* is not well-founded. The same is true of *Anoplolepis*, the other beneficial species; although more often associated with creeper growth than *Occophylla*, it is rather less so than *Pheidole* and *Iridomyrmex*, and so it also would be less likely to be encouraged by creepers than the harmful species.

Experiments on Vegetation.

Vegetation Control by 'Brushing'.

In order to attempt to get more direct information on the effect of creepers on ant distribution, certain overgrown areas of plantations were selected, and in certain plots in these areas ('brushed' plots) all shrubs and trees were cut down, all creepers were removed from the palm trunks, and ground vegetation was cut down close to the ground; this condition was maintained by repeated 'brushing' for a long time. The 'brushed' plots were all situated astride the border-line between areas occupied by different species of ants, so that, by comparison of changes in population in 'brushed' areas with those in the 'unbrushed' areas between them, it would be possible to see if good maintenance would favour the spread of one species into the territory of the other.

Two principal experiments on these lines were carried out, one at Tenaru, involving *Iridomyrmex myrmecodiae* and *Anoplolepis longipes*, and the other at Rua Vatu, involving *Pheidole megacephala* and *Occophylla smaragdina*.

(*a*) *The Tenaru ' brushing ' experiment.*

This was carried out in the eastern half of the large *Iridomyrmex* area (TX) at Tenaru. A series of five ' brushed ' plots were started in May and July 1955 (fig. 3, B.1–B.5); they were kept regularly ' brushed ' until November 1956

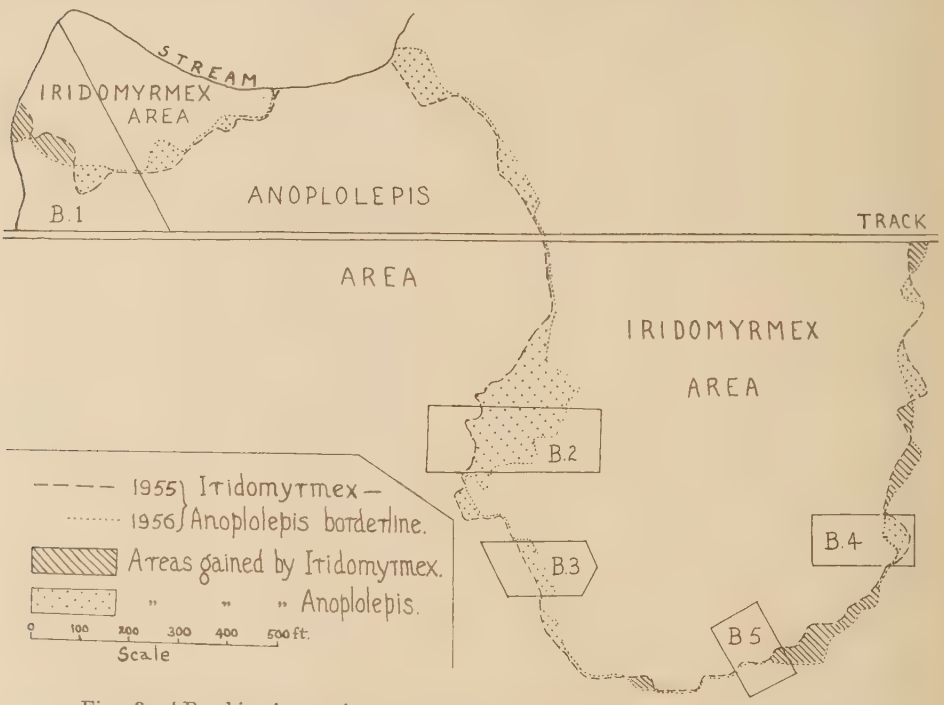


Fig. 3.—' Brushing ' experiment at Tenaru, showing the border-line between *Iridomyrmex myrmecodiae* and *Anoplolepis longipes* in May 1955, and again in November 1956. B.1—B.5 are plots which were kept ' brushed ' (free from undergrowth and creepers) during this period, while the remainder of the area was not so treated, and creepers and ground vegetation were allowed to grow unchecked.

(*i.e.*, for about 18 months); the rest of the area was left ' unbrushed ' so that creepers and other vegetation were not discouraged. The ' brushing ' operation included cleaning the bases of the trunks of the palms with wire brushes, so that the ' earthen ' runways of *Iridomyrmex* were removed and the ants were left unprotected against attack by *Anoplolepis*. It was expected that this procedure might open the way for attack by *Anoplolepis* (which was in any case extending its range at certain points), so that it would advance more rapidly in the ' brushed ' plots than in the ' unbrushed ' areas between.

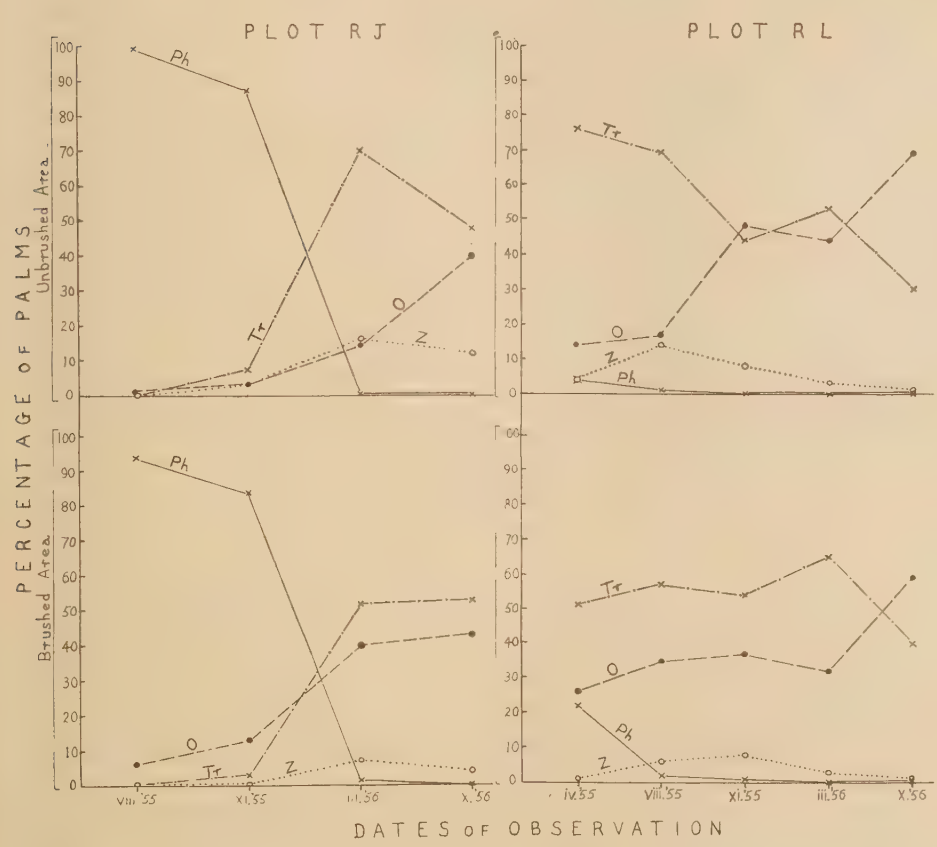
The ant distribution across the border-line was checked and plotted, palm by palm, at regular intervals, and at the end of the period the situation, as indicated by the total numbers of palms gained by each species, was as follows:

' Brushed ' plots		' Unbrushed ' area	
Gains by *Iridomyrmex*	Gains by *Anoplolepis*	Gains by *Iridomyrmex*	Gains by *Anoplolepis*
8	30	14	44

It can be seen that the *relative* numbers of gains by the two ants was very similar in the ' brushed ' plots and in the ' unbrushed ' area, the gains by *Anoplolepis* being 3·75 times as many as those by *Iridomyrmex* in the former, and 3·14 times as many in the latter. The actual areas involved are indicated in fig. 3. One may deduce from this that the amount of vegetation made little if any difference in this case to the relations between *Anoplolepis* and *Iridomyrmex*, or to the rate of advance of the former into the latter's territory.

(*b*) *The Rua Vatu ' brushing ' experiments.*

These experiments were done in an area where *Oecophylla smaragdina* was rapidly replacing *Pheidole megacephala*. The replacement was not a direct one in this case, since, in most cases at all events, other ' minor ' species of ants (referred to here as ' transitional ' species) occupied the palms in an intermediate stage; and, in some cases at least, after the disappearance of *Pheidole*, palms



Figs. 4–5.—' Brushing ' experiments in plots RJ and RL at Rua Vatu (Guadalcanal). The percentages of palms in the following conditions on the dates indicated are shown: Ph, with *Pheidole megacephala* dominant; O, with *Oecophylla smaragdina* dominant; Tr, with ' transitional ' species of ants dominant; Z, without any ants established. Figures for ' brushed ' and ' unbrushed ' areas are shown separately.

remained vacant for a period before being occupied in strength by another species. This type of replacement will be referred to in greater detail later.

The vegetation at the start of the experiment consisted mainly of wild gingers (*Curcuma* sp. and *Alpinia* sp.) and formed a dense growth 10–15 ft. high (Pl. XII, fig. 4), providing ample runways for *Oecophylla*. Creepers (*Piper* spp., *Epipremnum pinnatum* and a few Leguminosae) were also abundant. The 'brushed' plots were larger than those at Tenaru, and were oblong and rectangular, situated with their long axes running across the transition zone where the changes in ant population described above were taking place. Two such plots, RJ and RL, were cleared of vegetation in August and April 1955, respectively (Pl. XIII, fig. 1); 'brushing' involved the complete cutting down of all wild ginger, creepers and other vegetation so that anything which could be used by *Oecophylla* as a bridge from one palm to another was destroyed. RJ contained about 185 palms (3·4 acres) and RL 150 palms (2·7 acres). Alongside each, an 'unbrushed' control plot of equal size was marked out. These plots were examined palm by palm at intervals of a few months until October 1956, and the species of ant present on each were recorded. The results obtained are given in figs. 4 and 5, in which the percentages of palms in the following four categories are shown at each examination: (1) with *Pheidole* dominant, (2) with *Oecophylla* dominant, (3) with one or other 'transition' species dominant, and (4) without any ants present.

It can be seen at a glance that the history of the ant population in each 'brushed' plot is essentially identical with that of the 'unbrushed' control plot alongside it. Plot RJ (fig. 4) started with a very high percentage of palms occupied by *Pheidole* (99 and 94% in the 'unbrushed' and 'brushed' areas, respectively), and very few occupied by *Oecophylla* (1 and 6% respectively). After three months there was a very rapid reduction in *Pheidole*, which after a further four months could only be found on one or two palms; there was a corresponding increase in the other ants, with always a small proportion of palms without any ants. The transition species at first increased faster than *Oecophylla*, but this was later followed by a relative increase of the latter. Although *Oecophylla* made a more rapid increase during the last seven months in the 'unbrushed' than in the 'brushed' area, the final position after 14 months was very similar in both, as shown by the following figures:—

	Percentage of palms			
	with *Pheidole*	with *Oecophylla*	with transitional species	without ants
'Unbrushed' area	0	40	48	12
'Brushed' area	0	43	53	4

Plot RL (fig. 5) started at a later stage of a similar replacement process, when *Pheidole* had already been reduced considerably (occupying 4 and 22% in 'unbrushed' and 'brushed' areas, respectively), and transitional species were well established and *Oecophylla* was on the increase. It was, in fact, approaching the stage at which observations on plot RJ left off. During the total period of observation, *Pheidole* completely disappeared in both 'brushed' and 'unbrushed' areas; there was a decrease in transitional species and a corresponding

increase in *Oecophylla*, and although the latter was greater in the ' unbrushed ' than in the ' brushed ' areas, the final position in both was not so very different: —

	Percentage of palms			
	with *Pheidole*	with *Oecophylla*	with transitional species	without ants
' Unbrushed ' area	0	69	30	1
' Brushed ' area	0	59	40	1

Here, therefore, as at Tenaru, it is clear that the presence or absence of vegetation which may serve as a bridge from one palm to another has little if any effect on the course of a change over in ant populations that is already taking place. The Rua Vatu experiments are of special interest because they involve *Oecophllya* and *Pheidole*, and according to the creeper theory, the presence of climbing plants should favour *Oecophylla* and their absence should favour *Pheidole*. It might therefore be expected that removal of the creepers and other vegetation would arrest the decline of *Pheidole* and even help it to become re-established on palms which it had left. However, it had no such effect, because *Pheidole* disappeared with equal rapidity in both ' unbrushed ' and ' brushed ' areas. It is true that *Oecophylla* increased somewhat more rapidly in the ' unbrushed ' areas (especially in plot RL), but the final status was essentially similar under both conditions.

These experiments, as far as they go, therefore strongly suggest that ' brushing ' has little influence on changes in ant populations that are already taking place as the result of other causes. This is an important conclusion, because the creeper theory has been responsible for the spread of an idea that it is beneficial to leave plantations ' unbrushed ', on the grounds that under the overgrown conditions which result, the beneficial *Oecophylla* will replace the harmful *Pheidole* more readily; and that it is therefore dangerous to keep plantations in a well maintained condition since this may favour *Pheidole* at the expense of *Oecophylla*. It is suggested that there is no good reason for holding such views.

Transplantation of *Oecophylla* Nests.

Although not directly related to the effects of vegetation, certain experiments on nest transplantation involved the establishment of artificial runways to fulfil the supposed functions (according to the creeper theory) of climbing plants in promoting the spread of *Oecophylla*, so that they may be conveniently discussed here.

The idea has been entertained for some years that *Oecophylla* might be established in areas occupied by *Pheidole* by transplanting whole nests, taken from other localities, on to the palms. Experiments carried out by planters met with very varied results, although success has been claimed in some cases.

O'Connor & Leach (unpublished) put this idea to experimental test in 1948. Nests of *Oecophylla* were transplanted on to the trunks of six separate palms in *Pheidole* areas, three at Kukum and three at Lunga. Each of these palms was connected by fallen coconut fronds (which are favoured by *Oecophylla* as runways) with a number of other adjacent palms; some of these fronds were leant up against the trunks of the palms, to form bridges by which the *Oecophylla* could by-pass the *Pheidole* colonies at the bases of the trunks. After six weeks

the *Oecophylla* had apparently become established, and there the matter rested until four years later, when Phillips (unpublished) found that, of the six palms, four were occupied by *Anoplolepis*, one by *Iridomyrmex* and only one by *Oecophylla*.

In 1954, the author found the position to be the same as in 1952. The palms concerned, together with the distribution of ants on the palms with which they had been connected, and on some other adjacent palms are shown in fig. 6. It can

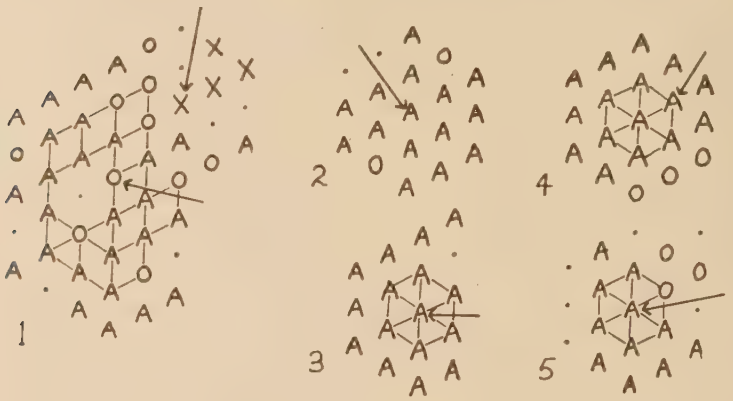


Fig. 6.—Coconut palms (marked with an arrow) on to which nests of *Oecophylla* were transplanted in 1948; thin lines indicate bridges made from fallen fronds, by which they were connected to adjacent palms. Letters indicate the species of ant occupying each palm in 1954: A, *Anoplolepis longipes*; O, *Oecophylla smaragdina*; X, *Iridomyrmex myrmecodiae*. Missing palms are indicated by a point.

be seen that the distribution of the few palms occupied by *Oecophylla* bears little if any relation to those on to which the *Oecophylla* nests were originally introduced. There were, in fact, no more *Oecophylla* in the neighbourhood of these palms than there were in other parts of the plantations (*cf.* fig. 1) and its distribution conformed to what was typical for *Oecophylla* in 1954, and was the result of a general and widespread change that had been taking place in the plantations; the introduction of *Oecophylla* locally had not influenced the situation.

Although limited in scope, therefore, this experiment indicates that although the transplantation of *Oecophylla* nests, at least on a small scale, may meet with an apparent temporary success, it is not likely to have any effect in the long run. Whether such an introduction on a much larger scale would have permanent results is not known; it would be a big undertaking, and has not yet been tried.

Ant Succession.

We have seen, in the foregoing pages, evidence of extensive changes in the composition of ant populations, and that these changes may in some cases take place very rapidly. Attempts to explain these changes as the results of environmental factors have so far met with little success.

The most spectacular, as well as the most economically important example of a change which has been observed with any degree of accuracy and detail is that which took place during the post-war years in the Kukum/Lunga/Tenaru group of plantations of Guadalcanal, where *Pheidole megacephala* had been predominant in the 1930's, and production of copra through nutfall had at one stage reached

the low average figure of 2·7 cwt. per acre. When O'Connor and Leach investigated these plantations in 1948, there had been a large measure of recovery from nutfall, and associated with this was the appearance of *Oecophylla*; the extent of increase in crops in an area was related to the degree of establishment of this ant. It was assumed that the replacement had been a direct one, the *Oecophylla* penetrating areas of *Pheidole* and even driving it out. Investigations were therefore naturally directed towards finding an explanation for the change, and attention was given to the unusual conditions imposed as the result of the war. Hence we have the creeper theory of O'Connor and Leach, based on the overgrowth of vegetation through lack of maintenance, and the insecticide theory of Phillips, based on the regular aerial application of DDT throughout this area by the United States Forces for control of mosquitos (see p. 524 for a fuller statement of these theories).

It may be that a direct change from *Pheidole* to *Oecophlla* did in fact take place to some extent, but detailed investigations at Rua Vatu have shown that in

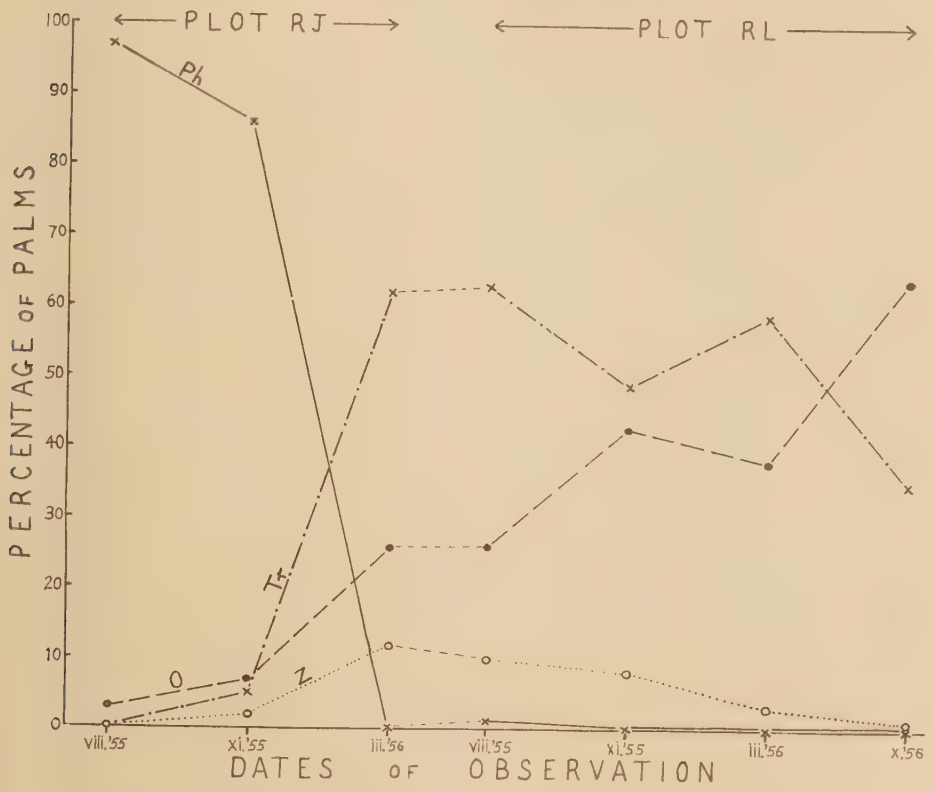


Fig. 7.—Graph showing the main trends in succession of ants in Rua Vatu plantation (Guadalcanal), starting with *Pheidole megacephala* dominant and ending with *Oecophylla smaragdina* dominant. The graph is a composite one, from detailed observations made on two plots (RJ and RL), showing percentages of palms in the following condition on the dates indicated: Ph, with *Pheidole megacephala* dominant; O, with *Oecophylla smaragdina* dominant; Tr, with transitional species of ants dominant; Z, without any ants established. Figures for 'brushed' and 'unbrushed' areas of the plots have been combined (*cf.* figs. 4 and 5).

TABLE X.

Ant succession in plot RJ (Rua Vatu). On the left are the more important species of ant present: the figures show the number of occasions on which each of the species at the top of the table had replaced those on the left, on individual palms, at the next examination.

Species of ant present at last examination	Species of ant present at next examination										
	No ants present	*Ireneidris myops*	*Paratrechina vividula*	*Bothriomyrmex pusillus* / *Paratrechina minutula* ssp. *atoma*	*Pheidolacanthinus sexspinosus*	*Tapinoma melanocephalum*	*Technomyrmex detorquens*	*Pheidole oceanica*	*Polyrhachis salomo*	*Anoplolepis longipes*	*Oecophylla smaragdina*
Pheidole megacephala ..	32	37	80	96	6	2	60	—	9	—	96
No ants present ..	—	2	1	7	—	2	10	4	—	—	11
Ireneidris myops ..	5	—	3	11	—	—	6	1	1	1	12
Paratrechina vividula ..	2	—	—	14	—	3	16	8	1	2	17
Bothriomyrmex pusillus / *Paratrechina minutula* ssp. *atoma*	3	3	5	—	6	—	22	4	3	3	28
Technomyrmex detorquens	6	—	1	7	3	—	—	8	1	8	40
Oecophylla smaragdina ..	7	2	2	10	5	1	27	3	2	6	—

this case there was a change of an indirect nature. Furthermore, in this plantation, recovery from nutfall did not occur until several years later, the greater part of it taking place between 1954 and 1956. Aerial insecticide application was never used there, so that the insecticide theory cannot be adduced as an explanation of the change. Admittedly the plantation was still in an overgrown condition, but the ' brushing ' experiments described above showed that this is unlikely to have been the cause of a replacement of *Pheidole* by *Oecophylla*. The rapidity of the disappearance of *Pheidole*, however, was such that, whereas it occupied in strength 72 per cent. of the total area of the plantation in August 1953 (from figures given by Mr. A. H. Green), by October 1956 it was with difficulty that *Pheidole megacephala* could be found.

Facts already given in describing the ' brushing ' experiments at Rua Vatu show that certain transitional species of ants usually first replaced *Pheidole*, and were in turn mostly replaced by *Oecophylla*. There was thus a succession of species, culminating with *Oecophylla* in most areas. The resultant recovery from nutfall was already well advanced in 1956. Further details of this succession will now be given.

The general nature of the succession is illustrated in figs. 4 and 5 already referred to. There is a very rapid decrease in *Pheidole*, accompanied by an almost equally rapid increase in transitional species, a less rapid increase in *Oecophylla* and at the same time the appearance of a number of unoccupied palms. Later, *Oecophylla* achieves further increase, while there is a corresponding decline in transitional species and unoccupied palms. Plots RJ (fig. 4) and RL (fig. 5) were, respectively, in earlier and later stages of this process at the time that they were studied, with some overlap between the later stages of RJ and the earlier stages of RL; so that by taking the first part of fig. 4 and the last part of fig. 5, and combining the figures for ' brushed ' and ' unbrushed ' areas (which, as already pointed out, are not essentially different), we can obtain a composite picture which shows the whole story (fig. 7), beginning with the dominance of *Pheidole* and ending with that of *Oecophylla*. The fact that the conditions in plot RJ in March 1956, and in plot RL in August 1955, were almost identical indicates that very similar changes were taking place widely in the plantation. There was a slight apparent check in the advance of *Oecophylla* in plot RL in March 1956; this was probably not real, but due to variations occurring in *Oecophylla* counts from day to day owing to weather conditions; wet weather discourages these ants from foraging, so that they may not be observed on all the palms included in the territory of each nest.

Of the transitional species, some are of much greater importance than others. The following figures, taken from five transitional areas in Rua Vatu plantation, including plots RJ and RL mentioned above, represent the total number of occasions on which various transitional species were found as dominant ants on individual palms; the species are listed in order of their importance, as judged from the total occurrences.

Technomyrmex detorquens (Wlk.)	542
* *Bothriomyrmex pusillus* (Mayr)	313
* *Paratrechina minutula* (Forel) ssp. *atoma* Forel	
Paratrechina manni Donisthorpe	139
Ireneidris myops Donisthorpe	101
Paratrechina vividula (Nyl.)	98
Pheidole oceanica Mayr	76

* Figures for these two species are added together since they are very similar and there was at first some confusion between them in the field; *Paratrechina minutula* was probably the more abundant.

Polyrhachis salomo Forel	75
Camponotus reticulatus Roger var. *bedoti* Emery	45
Tapinoma melanocephalum (F.)	14
Camponotus irritans (F.Sm.) var. *samoaensis* Santschi	13
Polyrhachis annae Mann	9
Odontomachus haematodes (L.)	4
Pheidole umbonata Mayr	1
Strumigenys sp. ? *godeffroyi* Mayr	1
Odontomachus sp. ? *saevissimus* (F.Sm.)	1
No ants present	133

A few other species, such as *Polyrhachis osae* Mann and *Pheidolacanthinus sexspinosus* (Mayr) occurred, but not as dominant species on the palms.

It is clear that only about eight species are of any importance to judge from their numbers. Their importance as far as protection against *Amblypelta* is concerned has been discussed in Part I (Brown, 1959). Some species (*Polyrhachis* and *Camponotus* spp.) are by no means confined to transitional areas, but may occur in small numbers anywhere. The species which are most characteristic of transitional areas are *Technomyrmex detorquens*, *Bothriomyrmex pusillus*, *Paratrechina minutula*, *P. manni* and *P. vividula*, *Ireneidris myops*, *Pheidole oceanica* and *Tapinoma melanocephalum*. *T. detorquens*, *B. pusillus*, *P. minutula*, *P. manni* and *Ph. oceanica* are of most interest because they forage up the trunks of the palms, especially when creepers are present; the other species (except for *Polyrhachis* and *Camponotus* spp.) are confined to nests in and around the roots at the base of the trunk.

It is interesting to note the large number of palms without any ants present during the transitional period, indicating that there is, sometimes at all events, an unoccupied stage, between the disappearance of one species and occupation by another.

By regular examination of transitional areas an attempt was made to discover more details about the succession of transitional species. Plot RJ is used for this purpose, being the only one for which sufficient records were made and in which at the same time *Pheidole* was well represented at the beginning and *Oecophylla* at the end of the period of observation. We are therefore concerned here only with such transitional species as occur in this plot, but it includes most of the more important ones; a few, such as *Paratrechina manni* and *Pheidole oceanica*, were relatively scarce, and significant figures were not obtained for them. In Table X, figures are given showing the number of occasions, on individual palms, when each of the main species of ant was found to have been replaced by another species at the next examination; these figures are obtained by adding together the changes recorded at the second, third and fourth examinations of the plot. Thus we find that *Pheidole megacephala* was replaced by *Ireneidris myops* on 37 occasions, by *Paratrechina vividula* on 80, by either *Bothriomyrmex pusillus* or *Paratrechina minutula* (these two species were not reliably distinguishable in the field) on 96 occasions, and so on. On 96 occasions it was found to have been replaced by *Oecophylla*, which represents about 23 per cent. of the total replacements recorded; on all the other 418 occasions when it had disappeared, it had either been replaced by other species or the palms had been left unoccupied. This means that *Pheidole megacephala* was not normally replaced directly by *Oecophylla*; in fact, changes were taking place so rapidly that it is probable that even on many of the 96 occasions when it was observed to have been replaced by *Oecophylla*, other (transitional) species had actually occupied the palms at some period between the two observations. Of the 55 occasions when unoccupied palms

were observed, 32 (approximately 53%) followed occupation by *Pheidole megacephala*. Again, in view of the rapidity with which changes were occurring, it is probable that on many more occasions there had actually been a period in between two examinations when the palms had been unoccupied. This suggests that *Pheidole* was, to a large extent at all events, dying off from other unknown causes, rather than being forcibly driven out by other species of ants. The latter were merely enabled to occupy a habitat which had been vacated by the previous disappearance of *Pheidole*.

If this is true, it presents a very different picture from that of direct strife between *Pheidole* and *Oecophylla* which has been visualised in the creeper theory to explain recovery from nutfall associated with *Pheidole*. The picture is one of disappearance and subsequent replacement, rather than of active replacement in battle. The replacement is usually first by other species and not by *Oecophylla*. The other figures in Table X give some indication of the succession of species which took place in plot RJ before the final establishment of *Oecophylla*, although the order of appearance is obviously subject to considerable variation. The species which most often follow after *Pheidole megacephala* are *Ireneidris myops*, *Paratrechina vividula*, and either *P. minutula* or *Bothriomyrmex pusillus*, with some indication of their arrival in this order, since the two last species more frequently follow *Ireneidris myops* or *Paratrechina vividula* than the reverse, and *Paratrechina vividula* occasionally follows *Ireneidris myops* but the reverse was never recorded. *Technomyrmex detorquens* was frequently found to follow *Pheidole megacephala*, but since it also very frequently followed after *Paratrechina vividula* and still more often after *Bothriomyrmex pusillus* or *P. minutula*, it appears normally to arrive later in the succession; it is probable that on many of the 60 occasions when it was recorded as following directly after *Pheidole megacephala*, other earlier species had in fact been in occupation at some intermediate period. *Pheidolacanthinus sexspinosus* and *Tapinoma melanocephalum* were too scarce for the figures to be significant; the same is true of *Pheidole oceanica*, but the fact that it never followed after *Pheidole megacephala*, and several times followed even after *Technomyrmex*, suggests that it appears very late in the succession.

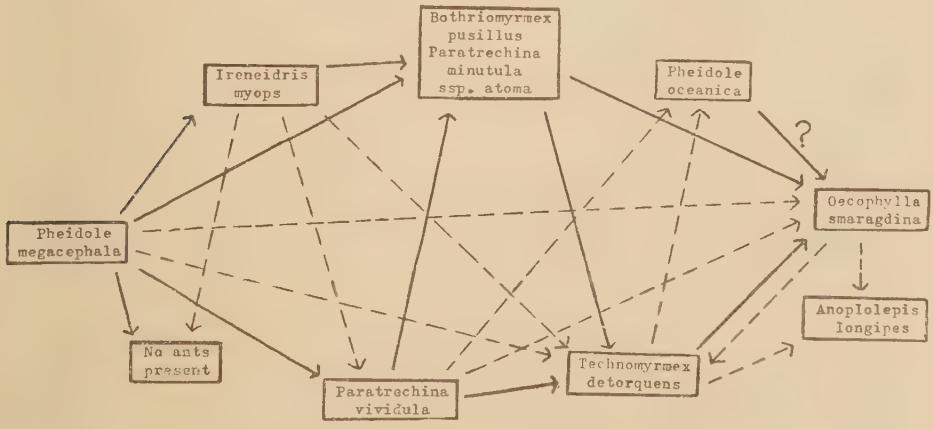


Fig. 8.—Diagram showing the main trends in succession of ant species in plot RJ in Rua Vatu plantation (Guadalcanal), from *Pheidole megacephala* through various transitional species to *Oecophylla smaragdina*. The most important stages in succession are indicated by unbroken lines, and less important ones by broken lines.

Apart from the 96 occasions when *Oecophylla* was recorded as following after *Pheidole megacephala* (commented on above), it most often succeeded *Technomyrmex*, corroborating the conclusion that of the more abundant transitional species the latter comes last in the succession. In one area *Anoplolepis longipes* occurred, and here it, and not *Oecophylla*, tended to replace *Technomyrmex*; or sometimes it replaced *Oecophylla* after the latter had first replaced transitional species. The fact that palms in which *Oecophylla* had occurred very frequently reverted (probably temporarily) to occupation by *Technomyrmex*, and less frequently by other transitional species, indicates that it may be some time before *Oecophylla* becomes firmly established.

The list of ants on the left of Table X, therefore, probably represents the most frequent order of succession in plot RJ, and an attempt has been made to put this in the form of a diagram (fig. 8), in which only the principal changes are indicated.

There is no precise information from plantations other than Rua Vatu to indicate that a similar form of succession has occurred elsewhere, but there is a little circumstantial evidence which may be mentioned. In the Kukum/Lunga Tenaru group of Guadalcanal, the major part of plot TO at Tenaru (which was recovering from nutfall) consisted, in 1948, of palms occupied by *Oecophylla*, or to a lesser extent "*Pheidole megacephala*", but an irregular group of 25 palms in one area was occupied by *Technomyrmex detorquens*; in 1954, the latter ant had disappeared and the palms were occupied mainly by *Anoplolepis longipes*, and a few by *Oecophylla*. *Technomyrmex* had, therefore, appeared in an intermediate stage as a transitional species; it is also very probable that many of the "*Pheidole*" palms of 1948 had been recorded as the result of misidentification, and that other transitional species had also been present; so that the area at that time may well have been in a condition similar to an intermediate stage at Rua Vatu, as recorded above. The succession in this event would have differed only from that recorded at Rua Vatu in that *Oecophylla* ultimately gave place to *Anoplolepis* on a much larger scale.

Another Guadalcanal plantation of interest is Rere, which according to report had undergone a recovery from nutfall in recent years, similar to that occurring at Rua Vatu more recently. A central area was stated to have suffered badly from nutfall about four years before; at my examination in 1955, two small patches occupied by *Pheidole megacephala* were found in this area, one of which was suffering slightly from nutfall; the adjacent palms were occupied by a mixed ant population, which included among others the typical transition species *Pheidole oceanica*, *Pheidole umbonata*, *Pheidolacanthinus sexspinosus*, *Paratrechina vividula*, *Paratrechina manni*, *Technomyrmex detorquens* and *Bothriomyrmex pusillus*. The coastal areas of the plantation were occupied mainly by *Oecophylla* and *Anoplolepis*, but there was one patch occupied by *Technomyrmex detorquens*. It is therefore probable that the nutfall occurring earlier had been associated with dominance of *Pheidole megacephala*, which had been almost completely replaced by a succession of transition species culminating with *Technomyrmex*, *Oecophylla* and *Anoplolepis*. This would present exactly the same picture as Rua Vatu.

In the Russell Islands, there is evidence of a similar succession in a plot in Faielau plantation. In 1948, most of the palms were recorded as occupied by *Pheidole megacephala*, but *Oecophylla* had started to appear; in 1952, some ants collected by Phillips and labelled "Faielau *Pheidole*" were found to be *Paratrechina vividula* (see p. 527), in 1954, and again in 1955, the author found *Pheidole megacephala* restricted to very few palms, but there were several occupied by *Paratrechina vividula* and *Bothriomyrmex pusillus*, two typical transition species; the majority of palms were by now, however, occupied by *Oecophylla*. It seems, therefore, that *Paratrechina* and *Bothriomyrmex* had played, at least to some extent, an intermediate rôle in a succession beginning with *Pheidole* and ending with *Oecophylla*; in another part of the plantation,

Occophylla was being replaced in 1955 by *Anoplolepis*, so that the picture comes to resemble that in some of the Guadalcanal plantations.

In the case of the reverse change, when an area occupied by *Oecophylla* changes to one of *Pheidole megacephala*, there is little precise evidence to go on, but it seems, to judge from the battles observed between the two ants in plot LQ at Lunga (p. 534) that the replacement in this case is a direct one; however, the considerable number of unoccupied palms at certain stages of the replacement (Table V) suggests that even here the arrival of one ant sometimes follows at some interval after the disappearance of the other, although transition species did not make their appearance in any numbers.

' Background ' terrestrial Ant Populations.

One may well ask where the transitional species of ants come from, when they become temporarily dominant during the brief interval between the disappearance of one major species and the appearance of another. Many of them are terrestrial, ground-nesting species, and can be found on the ground between the palms even in plantations in which the palms themselves are dominated by a major species. In a part of Kukum plantation where the palms were occupied by *Oecophylla*, and by *Anoplolepis* in an adjacent area, the ground was searched in an area between a group of 19 palms (about 0·22 acre), and the following numbers of nests of different species of ant were found:—

Pheidole nindi Mann	49
Tapinoma melanocephalum (F.)	15
Pheidole umbonata Mayr	6
Paratrechina vividula (Nyl.)	4
Ireneidris myops Donisthorpe	2
Cardiocondyla nuda Mayr	2
Paratrechina minutula (Forel) ssp. *atoma* Forel	1

Five of these seven species have already been listed as transitional species at Rua Vatu; the other two (*Pheidole nindi* and *Cardiocondyla nuda*) were found on coconut palms in other plantations.

In addition to the above ants, on the side of the plot nearest to the *Anoplolepis* area, *Anoplolepis* itself was found in 58 places on the ground; in 49 of these, brood was found together with the workers, and, in three, queens were present. This indicates that when *Anoplolepis* invades an *Occophylla* area it first gets well established on the ground, and when sufficiently numerous in its strongholds there it assails the palms themselves.

There is little doubt that most of the transitional species of ants, except possibly *Technomyrmex detorquens*, exist in small numbers on the ground almost everywhere as an indigenous, semi-natural community. Only when the numerical strength of the major species which is dominant on the palms declines are they able to invade the palm trunks in sufficient numbers to become conspicuous; members of a more or less regular succession of species then replace one another until they finally give place to another major species.

The reasons for the sudden decline in numbers of *Pheidole megacephala* at Rua Vatu (and probably in other areas also) are unknown; but they would appear to be of an intrinsic nature, since it has been shown that it was neither due to direct competition with other ants, nor to changes in the vegetation. The fact that the ant had become extremely abundant before the decline suggests that some cause resulting from over-population was responsible, and one is tempted to put forward as an explanation some form of epidemic; there was no obvious evidence of it, but the matter was not investigated.

Summary.

In the British Solomon Islands Protectorate, the incidence of immature nutfall of cococuts that is caused by the Coreid bug, *Amblypelta* (chiefly *A. cocophaga* China), depends indirectly upon certain species of ants, some of which protect the palms against *Amblypelta*, whilst others do not. There is evidence that populations of the ants can sometimes change quite rapidly, and that local fluctuations in nutfall are largely dependent on such changes.

Observations on ant populations were maintained over a period of $2\frac{1}{2}$ years (1954–1956) to find out if such changes are of common occurrence and to attempt to explain their cause.

An account is given of ideas, current at the beginning of the author's investigation, on the effect of vegetation and other factors on changes in ant populations, and in particular of the cover-crop or creeper theory, the advocates of which suggest that the presence of such vegetation, prevalent in plantations during and after the war, provided conditions favourable to beneficial species of ants.

The actual progress of recorded changes in ant populations is described and discussed. Rapidly changing populations usually involve the ants, *Pheidole megacephala* (F.), *Oecophylla smaragdina* (F.), and sometimes also *Anoplolepis longipes* (Jerd.); more stable populations usually involve *Iridomyrmex myrmecodiae* Emery, and occasionally *Oecophylla* and *Anoplolepis*. An account is given of the 'battles' which often occur during replacements of one species by another.

An account is given of the vegetation found in coconut plantations in the Solomon Islands, with special reference to the plant communities associated with each of the four species of ant of special importance in immature nutfall, and also with mixed ant populations. It is concluded that heavy creeper growth is not particularly associated with *O. smaragdina* (as was thought by supporters of the creeper theory), nor with the other beneficial species *A. longipes*, but rather, if anything, with *P. megacephala*, a non-protective or harmful species; there is thus no good reason to suppose that a growth of creepers will encourage beneficial species. *Iridomyrmex myrmecodiae* is the only species of the four which tends to be associated with a characteristic type of vegetation, including several species of epiphytes and often heavy creeper growth. But there are exceptions even to this, and there is evidence that the epiphytic vegetation may to some extent be the result rather than the cause of the presence of *Iridomyrmex*. There are, in fact, exceptions to every rule, and it is concluded that vegetation is not an important factor controlling ant distribution, except in so far as heavy growth of creepers and other plants may encourage a more mixed ant population in general, including several indigenous species which are not normally conspicuous in well-maintained plantations; if there is any effect on the four 'major' species, it is to encourage *Pheidole* and *Iridomyrmex* at the expense of *Oecophylla* and *Anoplolepis*.

An account is given of two experiments which involved control of creepers and other vegetation by repeated cutting down or 'brushing' in marginal zones between areas occupied by two different ant species, to see if this practice would alter the course of changes in population that were already taking place. One experiment involved a marginal zone between *I. myrmecodiae* and *A. longipes*, and the other between *O. smaragdina* and *P. megacephala*. It was found that in both cases there was no appreciable difference in the course of events between 'brushed' plots and plots adjacent to them in which the vegetation was not controlled. This bears out the previous conclusions that the presence or absence of creepers and other vegetation has little, if any, effect upon changes in ant populations.

At Rua Vatu, where an extensive replacement of *P. megacephala* by *O. smaragdina* was taking place, accompanied by recovery from a condition of heavy

nutfall, detailed studies revealed that this replacement was not a direct one, but that, at all events for the most part, a succession of normally unimportant ' transition ' species first replaced *Pheidole*, and were in turn replaced by *Oecophylla*. The details of this succession are described and discussed. Evidence is produced to suggest that a similar succession may have been involved in recorded examples of recovery from nutfall in other places, notably in that which occurred in the Kukum/Lunga/Tenaru group of plantations after the second world war. These conclusions present a picture not so much of direct antagonism between *Pheidole* and *Oecophylla*, but rather of the initial disappearance of *Pheidole* owing to unknown intrinsic factors, followed later by the infiltration of *Oecophylla* in the wake of a variable succession of indigenous ' transition ' species, which have been allowed to increase in numbers temporarily during the interim period when the area is not dominated by either of the two major species. In view of this, it is not so surprising that a factor such as vegetation should have little or no direct effect upon the change as suggested in terms of the creeper theory.

As regards the reverse change, the replacement of *Oecophylla* by *Pheidole*, there is little evidence to go on, but such as there is suggests that the replacement in this case is more in the nature of a direct one.

The fact that recovery from nutfall took place recently at Rua Vatu, at a time and place where insecticides had not been applied, contradicts the theory that the earlier and similar recovery in the Kukum/Lunga/Tenaru group of plantations was the result of a differential effect upon ant species of the application of insecticides during the war for mosquito control.

Acknowledgements.

In Part I of this work, acknowledgement was made to all those who had given me assistance in various ways. I would like here to repeat acknowledgement of my indebtedness to those same people, and more especially to Mr. G. E. J. Nixon, of the Commonwealth Institute of Entomology, who has shown unlimited patience in identifying innumerable samples of ants, and to Mr. A. H. Green, agronomist to Messrs. Levers' Pacific Plantations Pty Ltd., who gave much assistance in checking plots and provided invaluable information about the earlier history of certain important plots and plantations, apart from the benefit of his experience and opinions in discussion. Also, in connection especially with Part II, I would like to add certain names to my earlier acknowledgements; Mr. B. A. O'Connor, of the Department of Agriculture, Fiji, for the benefit of helpful discussion and suggestions, and the late Dr. J. S. Phillips for information in correspondence and unpublished reports; to Dr. E. J. H. Corner, of Cambridge, I am indebted for the identification of plants of the genus *Ficus*, and to Dr. G. Taylor (and later Mr. J. E. Dandy), Keeper of Botany at the British Museum (Natural History), and members of his staff for the identification of other plants; also to Mr. J. W. Parham of the Department of Agriculture, Fiji, and Mr. J. S. Womersley, of the Department of Forests, Territory of Papua and New Guinea, for assistance in plant identification. Finally I would like to thank Mr. E. O. Pearson, Director of the Commonwealth Institute of Entomology, for his interest and very helpful criticisms and suggestions.

References.

Brown, E. S. (1959). Immature nutfall of coconuts in the Solomon Islands. I. Distribution of nutfall in relation to that of *Amblypelta* and to certain species of ants.—*Bull. ent. Res.* **50** pp. 97–133.

O'Connor, B. A. (1950). Premature nutfall of coconuts in the British Solomon Islands Protectorate.—*Agric. J. Fiji* **21** pp. 21–42.

Phillips, J. S. (1956). Immature nutfall of coconuts in the British Solomon Islands Protectorate.—*Bull. ent. Res.* **47** pp. 575–595.

Way, M. J. (1954). Studies of the life history and ecology of the ant *Oecophylla longinoda* Latreille.—*Bull. ent. Res.* **45** pp. 93–112.

© Commonwealth Agricultural Bureaux, 1959.



FIG. 1. Battle between *Oecophylla smaragdina* and *Pheidole megacephala* on base of coconut trunk; *Pheidole* is 'entrenched' in the old termite runways in the bottom right-hand corner.



FIG. 2. *Epipremnum pinnatum* climbing up coconut trunk.



FIG. 3. Coconut trunk covered with creeping stems of *Epipremnum pinnatum* and *Piper* sp., exposed by removal of leaves.



FIG. 4. Thick stand of wild ginger (*Curcuma* sp.) in coconut plantation.



FIG. 1. Part of same area as Plate XII, fig. 4, with wild ginger cut down, and ground cleared ('brushed plot').



FIG. 2. A young plant of *Ficus tinctoria* epiphytic on coconut trunk.



FIG. 3. *Piper* sp. (below) and *Pyrrosia acrostichoides* (above) on coconut trunk.



FIG. 4. *Grammatophyllum* sp., an orchid, on coconut trunk.



FIG. 1. Leaves of *Dischidia milnei* and runways of *Iridomyrmex myrmecodiae* on coconut trunk.



FIG. 2. *Myrmecodia* sp. *cf. solomonensis* on coconut trunk.



FIG. 3. *Hydnophytum formicarium*, with part of tuberous base cut across to show network of cavities within.



FIG. 4. Pepesala (Russell Islands), with cattle. An *Oecophylla* area.



FIG. 1. Hulo (Baunani, Malaita): leguminous creepers, *Calopogonium mucunoides*, on bases of trunks should be noted. An *Anoplolepis* area.



FIG. 2. *Anoplolepis* feeding from extra-floral nectaries of *Cassia alata*.



FIG. 3. Rua Vatu (Guadalcanal): leguminous creepers on palm trunks (mainly *Centrosema* and *Pueraria*). A *Pheidole* area.



FIG. 4. Lunga (Guadalcanal): an area in which *Pheidole megacephala* had recently replaced *Anoplolepis longipes*.



FIG. 1. Creeper stems and termite runways utilised by *Pheidole megacephala*.



FIG. 2. Jack Harbour (Karikana, Kolombangara): *Stenochlaean juglandifolia* climbing up trunks. An *Iridomyrmex* area.



FIG. 3. Kau-Kau (Guadalcanal): *Oecophylla-Iridomyrmex* border-line (*Iridomyrmex*-occupied palms bearing epiphytes on trunks).



FIG. 4. Tenaru (Guadalcanal): an area recently occupied by *Iridomyrmex*.

IMMATURE NUTFALL OF COCONUTS IN THE SOLOMON ISLANDS.

III.—NOTES ON THE LIFE-HISTORY AND BIOLOGY OF *AMBLYPELTA*.

By E. S. Brown

Commonwealth Institute of Entomology.

(Plate XVII.)

Parts I and II of this series of papers (Brown, 1959*a*, *b*) each dealt with a specific aspect of the problem of immature nutfall. The present part covers a few miscellaneous items of general interest in the life-history and biology of *Amblypelta cocophaga* China. The food-plants of this and other members of the genus have been discussed in an earlier paper (Brown, 1958*b*).

Population Density.

The extremely low density of populations of *A. cocophaga* in the crowns of coconut palms, even in heavy nutfall areas, has always been a matter for surprise, and the fact that they can do serious damage at such low concentrations is one of the main factors which makes effective control very difficult.

It is no easy matter to make accurate counts of population density in palm crowns. Vanderplank (1958) has pointed out the difficulties of estimating numbers of a similar Coreid, *Pseudotheraptus wayi* Brown, on coconut palms in Zanzibar, and discussed the various methods which he tried. In the Solomon Islands the problem is rendered more difficult by the fact that many of the nutfall areas are dominated by the ant, *Iridomyrmex myrmecodiae* Emery, which swarms over the palms, and the attentions of which make life extremely unpleasant for climbers.

Some observations made during the course of insecticide trials at Mamara in Guadalcanal in June and July 1956 are worth recording, although only limited numbers of palms and insects are involved. The area was one of moderate nutfall (with approximately 50% loss of crop) associated with *I. myrmecodiae*. The palms were sprayed individually from the top of an extending ladder (Pl. XVII, fig. 1). Before the application, the operator spent a short time examining the central area of the crown, including all the spadices and frond-bases, and the distal parts of the fronds as far as they could be seen. The use of the ladder enabled the examination to be made with the minimum amount of disturbance to the crown, so that adults of *Amblypelta* were probably not often put to flight, as often happens when a climber ascends a palm.

Two adjacent areas were examined; area A covered 3·13 acres and contained 82 palms; area B covered 3·29 acres and contained 81 palms. The vidaka damage rate, ' V.D.R.', (Brown, 1959*a*, p. 109) for each area was estimated from all the fallen nutlets at the time of application. The figures obtained were as follows:—

Area	V.D.R.	No. of palms searched (N)	Total adults (a)	N/a	Total nymphs (n)	N/n	N/(a+n)
A	96·8	82	9	9	17	5	3
B	90·8	81	19	4	13	6	2·5

There was thus an average of one example of *Amblypelta* (either adult or nymph) for every 3 palms in area A, and every 2·5 palms in area B; adults were relatively scarcer, and nymphs slightly more numerous, in area A than in area B. The V.D.R. was high in both cases, but, curiously, somewhat higher in A where the total population density was slightly less. Even allowing for the possibility of as many as half of the insects being overlooked, there is still a density of less than one per palm. Both densities of nymphs and V.D.R. are somewhat higher than any of those recorded for *P. wayi* by Vanderplank (1958, Tables III–V).

Area A was given a second spraying with insecticide one month after the first, and a second count of *Amblypelta* was made at the same time. The figures obtained were as follows:—

V.D.R.	No. of palms searched (N)	Total adults (a)	N/a	Total nymphs (n)	N/n	N/(a+n)
84·7	82	8	10	17	5	3·3

It is seen that the density, both of adults and nymphs, is almost identical with that at the first examination. The spray used was 0·15 per cent. dieldrin emulsion concentrate; the treatment was thorough, and there is good reason to think that all nymphs and adults, at all events in the central part of the crown, were killed at the first treatment. This indicates that, during the interval of one month between treatments, adults had immigrated from outside the area to replenish the population up to the level of its original density, and that more nymphs had appeared. It was observed that, at the first examination, nymphs were of all instars except the first, while at the second only second- and third-instar nymphs were found. This suggests a reason for the reappearance of more nymphs, which will be discussed later in connection with life-history.

Life-history of *Amblypelta cocophaga* on Coconut Palms.

Oviposition, and the first nymphal instar.

There has always been some doubt as to what part of the coconut palm is mainly used by *Amblypelta* for oviposition. It is worth quoting from Phillips (1940, p. 309) for an account of the state of knowledge as it has existed up to now:

"Many vain searches were made for eggs, and very occasionally one or two were found on the young nut or on some other part of the spadix. Doubtless some are laid on the numerous male flowers which fall during the first two or three weeks of the life of the spadix. (In the laboratory this was often the case). It was not until early in 1938 that Mr. Love found that eggs were frequently laid on the leaflets of the central spike, *i.e.*, the new, unopened leaf. He also found nymphs on this part of the palm, and it seems likely that they migrate from here to the spadices. This seems to indicate that any form of control that only takes the spadices into account is doomed to failure.

"The life-history of a typical *Amblypelta* bug would thus be as follows:—The egg and first nymphal stages are spent on the central leaf-spike (10 days); then follows a period of wandering through the crown until the nymph reaches a young spadix; there it may remain feeding for the rest of its nymphal life. . . ."

The author's investigations have found this account to be only partly correct. But Phillips' statement (*loc. cit.*, p. 308), confirmed by the author, that first-instar nymphs are very rarely found on the spadices does suggest that the main oviposition site is somewhere else on the palm. In order to locate it, two palms in different nutfall areas of Guadalcanal, one at Kukum in April 1956 and one at

Tenaru in August 1956, were dissected and examined in detail; all the fronds, and all the spadices, and their sheaths, were cut off one at a time and lowered to the ground on a rope, in order to avoid dislodging any eggs which might be attached to them; they were then carefully examined on the ground. The fronds were examined in order from the oldest (lowest) to the youngest. The position of all eggs was noted.

The results are given in Table I. The total number of eggs found was 26 on the palm from Kukum, and 20 on that from Tenaru. Of these, 73 and 90 per cent., respectively, were on the fronds, the remainder being on the spadices. The former were not concentrated on the young fronds of the terminal spike, as stated by Phillips, but were more or less evenly distributed on old and young fronds, as the following figures show.

No. of frond (oldest first)	Number of eggs	
	Palm at Kukum	Palm at Tenaru
1– 8	4	3
9–16	7	6
17–24	5	6
25+	3	3

If anything, the greatest number was found on fronds of medium age. All were laid singly on the undersides of the leaflets, in the basal recess formed as the result of the Λ-shaped cross section of the leaflet (Pl. XVII, fig. 2). They were placed on leaflets at variable distances from the base of the frond, *i.e.*, from the centre of the palm crown. Eggs laid on the spadices were mainly at the bases of the branches, two being on old spadix sheaths.

It seems, therefore, that the basal recesses of the leaflets form the principal oviposition site on coconut palms. The habit is an adaptive one in that the site is the best protected position on the frond, both from physical damage due to wind action, since it is at the base of the leaflet and close to the midrib of the frond, and also from heavy rain since it is on the underside. Eggs laid on the spadices are also protected from physical damage, but not from rain and are possibly more subject to attack by predators. It is interesting that the habit seems to be so firmly incorporated into the behaviour of the insect, as this suggests that *Amblypelta* has been associated with coconut palms for a long time. It should be noted that these observations refer to the subspecies *A. cocophaga cocophaga* China (see Brown, 1958*a*); oviposition has not so far been studied in *A. c. malaitensis* Brown.

The prevalence of oviposition on the fronds at some distance out from the centre of the crown explains the scarcity of first-instar nymphs on the spadices. The first instar apparently feeds little or not at all, and, after hatching, it probably remains stationary at the point of hatching for some time, and then migrates slowly inwards towards the spadices, so that most of them will have attained the second instar by the time that they have reached them and will then start feeding. It explains also the reappearance of second- and third-instar nymphs on the spadices a month after spraying with dieldrin, as described earlier. These nymphs would have come from eggs already present on the underside of the fronds, and which are resistant to insecticide and in any case are protected from spray droplets which fall downwards by gravitation; nymphs which hatch after any residual effect has disappeared can migrate unharmed inwards towards the spadices.

Although the number of eggs counted seems large in proportion to the density of nymphs and adults, it should be noted that a high proportion either fail to

TABLE I.

Positions and details of *Amblypelta* eggs found on coconut palms from Kukum and Tenaru.

No. of frond (oldest first)	Palm at Kukum					Palm at Tenaru				
	No. of eggs	Hatched normally	Parasitised	Failed to hatch	Broken	No. of eggs	Hatched normally	Parasitised	Failed to hatch	Broken
1	—	—	—	—	—	—	—	—	—	—
2	1	—	—	—	1	—	—	—	—	—
3	1	—	1	—	—	1	—	1	—	—
4	—	—	—	—	—	1	—	1	—	—
5	1	—	1	—	—	—	—	—	—	—
6	1	—	—	—	1	—	—	—	—	—
7	—	—	—	—	—	—	—	—	—	—
8	—	—	—	—	—	1	1	—	—	—
9	—	—	—	—	—	1	1	—	—	—
10	—	—	—	—	—	1	—	1	—	—
11	1	—	—	1	—	1	1	—	—	—
12	3	2	—	—	1	—	—	—	—	—
13	—	—	—	—	—	1	—	1	—	—
14	—	—	—	—	—	1	—	1	—	—
15	2	1	—	1	—	1	1	—	—	—
16	1	—	1	—	—	—	—	—	—	—
17	—	—	—	—	—	1	—	1	—	—
18	—	—	—	—	—	—	—	—	—	—
19	—	—	—	—	—	—	—	—	—	—
20	1	—	—	1	—	1	—	—	1	—
21	1	—	—	1	—	1	—	1	—	—
22	1	—	1	—	—	1	—	1	—	—
23	1	—	—	1	—	1	—	1	—	—
24	1	—	—	1	—	1	—	1	—	—
25	1	—	—	1	—	1	—	1	—	—
26	—	—	—	—	—	—	—	—	—	—
27	2	—	—	1	1	2	—	—	2	—
28	—	—	—	—	—	—	—	—	—	—
Green spadices ..	6	2	—	4	—	1	1	—	—	—
Dry spadix sheaths ..	1	—	—	1	—	1	1	—	—	—
Total	26	5	4	13	4	20	6	11	3	0
		(19%)	(15·5%)	(50%)	(15·5%)		(30%)	(55%)	(15%)	(0%)

hatch, or are damaged or parasitised; from approximately one-fifth to one-third of the total represent eggs which "hatch normally" (Table I), and of these several had already hatched an indefinite period beforehand when examined.

Subsequently to the above observations, a procedure was frequently adopted, when examining palm crowns in nutfall areas for other purposes, of removing a limited number of fronds from each palm and examining them for eggs; these were usually taken from among those of intermediate age. These examinations supported in general what had been found before, in that the eggs were almost all in the basal recesses on the undersides of the leaflets, an occasional one being found on the upper surface of a leaflet. In general, the numbers found corresponded to considerably smaller densities than those recorded on the two palms specially examined. Assuming an average of 36 fronds per palm (possibly a slight over-estimate), the average number of eggs per palm for a small sample at Kukum on 2nd October 1956 was 8·3; for two larger samples in the same plot at Mamara in June and July 1956, the averages were only 5 and 5·4 eggs per palm, respectively; since only fronds were examined on this occasion, a small percentage should be added for the few eggs which may have been present on the spadices, but even so the density is very much less than in the two palms specially examined at Kukum and Tenaru.

On one occasion, two eggs were found in feeding scars of *Amblypelta* on nutlets which had fallen to the ground; they were presumably laid in the crowns before the nutlets fell.

Oviposition has not been specially studied on food-plants other than coconut, a list of which has been given by Brown (1958*b*); on *Manihot esculenta*, however, eggs have been observed on the stem under the base of the petiole (Pl. XVII, fig. 3).

In captivity, eggs are mainly laid on the walls of the cages, and occasionally on the body of other individuals of *Amblypelta* (Pl. XVII, fig. 4).

Parasites.

Phillips (1956, p. 576) has briefly reviewed attempts at biological control of *Amblypelta* by parasites. In view of the failure of earlier attempts at parasite control, little attention was given by the author to this aspect of the problem. The few observations which were made are, however, worth putting on record.

Egg-parasites.

Phillips (1941) has described his researches on the possibility of introducing egg-parasites of Dasynine bugs from the Netherlands Indies for the control of *Amblypelta*. These involved species of the parasite genera *Ooencyrtus*, *Hadronotus* and *Anastatus*.

The author's observations were concerned only with indigenous parasites, on which very little work has so far been done. Phillips (1941, p. 136) states that a species of *Anastatus* was hatched by Lever from a parasitised egg of *Amblypelta* from Kolombangara Island, but that he himself had failed to obtain parasites from eggs collected from Guadalcanal.

The more extensive collecting of eggs carried out by the author described in the foregoing pages enabled some assessment to be made of the status of egg-parasites in the Guadalcanal plantations. All eggs collected were kept in separate tubes to see whether they hatched normally or were parasitised. All parasites emerging were kept and later identified as the Eupelmid, *Anastatus axiagasti* Ferrière, including one or two individuals of var. *rufithorax* Ferrière from Mamara; other indigenous egg-parasites must therefore be rare or absent.

Many of the eggs found on the palms had already hatched. A study of the egg-shells left after normal hatching and after emergence of parasites in the laboratory showed that these could be readily distinguished. In normal hatching,

the operculum breaks away cleanly to leave a regular margin to the emergence hole; when a parasite emerges the operculum does not separate, but an irregular rupture of the shell is made, usually including a part of the operculum (fig. 1).

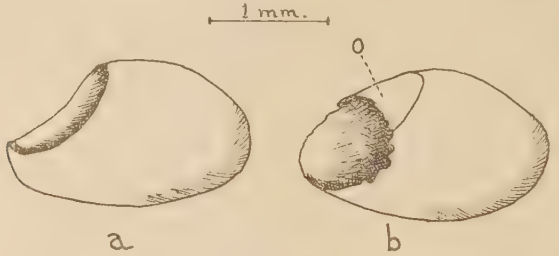


Fig. 1.—(a) egg-shell of *Amblypelta cocophaga cocophaga* after normal hatching; the operculum has broken away cleanly to leave an aperture with a regular margin; (b) egg-shell of the same species after emergence of the egg-parasite, *Anastatus axiagasti*; the irregularly broken margin of the emergence aperture should be noted; O, remaining part of operculum.

Thus it was usually possible to distinguish empty egg-shells, as well as unhatched eggs collected in the natural state, according to whether they had been parasitised or not. Some egg-shells had been considerably broken and damaged and it was impossible to classify them with certainty. Many of the unhatched eggs did not develop normally; they were discoloured, often of an opaque dark bronze hue, and without the characteristic eye-spots which can be seen in a normal egg; a bubble was often present in the fluid contents. Although several of such eggs eventually yielded parasites, it was impossible to say whether the failure of others to develop further was due to an abortive parasitisation or to other causes, and these eggs were therefore recorded as "failed to hatch" in Table I, which classifies quantitatively the eggs and egg-shells found on the two palms specially examined for eggs at Kukum and Tenaru. It will be seen from this table that, on the Kukum palm, 4 out of 26 eggs (15·5%) showed evidence of parasitism, while on the Tenaru palm there were as many as 11 out of 20 (55%). These figures may be regarded as minimal, since some of the eggs with broken shells, and those which failed to hatch, may also have been parasitised.

Fifty-three eggs collected on various occasions from palms at Kukum and Mamara were classified as follows:—

Hatched normally	Parasitised	Failed to hatch	Broken
20 (38%)	18 (34%)	9 (17%)	6 (11%)

The average rate of parasitisation for these and the eggs in Table I is 33 out of 99, or 33·3 per cent. This rate, although the figure as explained above is minimal, is evidently insufficient to bring about effective control; the thin distribution and dispersal of eggs must render higher rates improbable. Successful hatching of eggs from the above figures is only 31 out of 99, or 31·3 per cent. If this rate of hatching is sufficient to maintain a harmful (although small) population,

there do not appear to be any great possibilities for biological control through egg-parasites.

Parasites of the adults and nymphs.

In December 1949, O'Connor introduced the parasitic Tachinid fly, *Trichopoda pennipes* (F.), into an area of severe nutfall associated with the ant, *Iridomyrmex myrmecodiae*, at Baunani, Malaita. Phillips (1956) relates that many hundreds of examples of *Amblypelta* were collected there in 1951 and 1952, but that no parasitisation by *Trichopoda* was found. In September 1954, and May–June 1955, the author again collected some 500 adults of *Amblypelta*, with similar negative results. It is clear that the parasite has not survived, or if it has it is clearly not exercising any control over *Amblypelta*, for the population density of the latter is still relatively high, and nutfall still just as severe as before the introduction. It is possible that *Trichopoda* has survived in other hosts, such as the Pentatomid, *Axiagastus cambelli* Dist., but this was not investigated.

Predators.

Two predators that may have some slight influence on nutfall were observed; one a predator on *Amblypelta*, the other on the ant, *Oecophylla smaragdina* (F.).

The first is a Reduviid bug, which proved to be a new species, subsequently described as *Pristhesancus browni* Miller (1958). It is quite common generally in the plantations, but unlike other Reduviids it was found not uncommonly in the crowns of coconut palms in nutfall areas; the fact that nymphs were found there shows that it breeds in the palms. No direct evidence was obtained that it preys upon *Amblypelta* in the natural state, but it did so readily in cages in captivity, and there is little doubt that if it were more abundant it would exercise some measure of control.

The predator on *Oecophylla* is a Cheliferid or 'false scorpion', *Paratemnus salomonis* Beier. These small Arachnids live in crevices under the 'bark' on coconut trunks; they were found in Guadalcanal (Kukum), San Cristobal (Waimamura, Hawa), and the Russell Islands (Ufa, Faielau). Mostly they were found on palms occupied by *O. smaragdina*, but sometimes with *Anoplolepis longipes* (Jerd.). In either case the chelifer lies in wait at the entrance to a crevice, and when an ant walks over or investigates the crevice, catches hold of its appendages with its chelae, and holds it struggling until it succumbs; the body of the chelifer itself is protected within the crevice. On one occasion it occupied the same palm as the ant, *Tapinoma melanocephalum* (F.), which itself inhabits crevices; the chelifer and the ant on this occasion were almost invariably found in separate crevices.

At Hawa, another similar chelifer, *Parachernes* (*Argentochernes*) *insularis* Beier was found together with *Paratemnus* under the leaves of *Dischidia milnei* (Brown, 1959*b*, Pl. XIV, fig. 1).

It is possible that these Arachnids exercise some control over *Oecophylla*, which could be important since the latter exercises protection of palms against *Amblypelta*. In Zanzibar, *Oecophylla* has been found by Vanderplank (unpublished) to be similarly attacked by chelifers; specimens collected there by the author were identified as *Paratemnus cllingseni* Beier.

Summary.

Observations on the population density of *Amblypelta cocophaga* China on coconut palms in the Solomon Islands are described. Although the figures are somewhat larger than those previously reported for the related Coreid, *Pseudotheraptus wayi* Brown, in Zanzibar, the densities are still very low.

Observations were made on the oviposition habits of *A. cocophaga*. The principal oviposition site, contrary to previous observations, was found to be on

the undersides of the fronds, in the basal recesses of the leaflets. The first-instar nymphs on hatching have to make their way to the spadices in the centre of the palm crown; this explains why first-instar nymphs are themselves only rarely found on the spadices, and also why a single treatment with insecticide is not completely effective, since the oviposition sites escape the treatment. Observations on the number of eggs on coconut palms are recorded.

Anastatus axiagasti Ferrière was found to be a common egg-parasite of *Amblypelta cocophaga* in certain plantations of Guadalcanal. Rates of parasitisation on coconut palms ranged from 15·5 to 55 per cent. with an average of 33·3 per cent. The percentage of successful hatching of *Amblypelta* eggs ranged from 19 to 38 per cent., with an average of 31·3 per cent.

Investigation of the area of Baunani plantation in Malaita, where the Tachinid parasite, *Trichopoda pennipes* (F.), had been released in 1949, indicated that it has not survived there, or, if it has, is exercising no control over *A. cocophaga*.

Observations are recorded on two predators of interest with regard to immature nutfall.

Acknowledgements.

In addition to those whose assistance has already been acknowledged in Parts I and II of this series of papers, the author wishes to thank the following for their help in identification of the groups mentioned: Mr. R. D. Eady and Mr. N. C. E. Miller, both of the Commonwealth Institute of Entomology (Eupelmidae and Reduviidae, respectively), and Dr. M. Beier, Naturhistorisches Museum, Vienna (Cheliferidae).

References.

BROWN, E. S. (1958*a*). Revision of the genus *Amblypelta* Stål (Hemiptera, Coreidae).—*Bull. ent. Res.* **49** pp. 509–541.

BROWN, E. S. (1958*b*). Injury to cacao by *Amblypelta* Stål (Hemiptera, Coreidae) with a summary of food-plants of species of this genus.—*Bull. ent. Res.* **49** pp. 543–554.

BROWN, E. S. (1959*a*). Immature nutfall of coconuts in the Solomon Islands. I. Distribution of nutfall in relation to that of *Amblypelta* and to certain species of ants.—*Bull. ent. Res.* **50** pp. 97–133.

BROWN, E. S. (1959*b*). Immature nutfall of coconuts in the Solomon Islands. II. Changes in ant populations, and their relation to vegetation.—*Bull. ent. Res.* **50** pp. 523–558.

MILLER, N. C. E. (1958). Results of the Archbold Expeditions. On the Reduviidae of New Guinea and adjacent islands (Hemiptera-Heteroptera). Part 2.—*Nova Guinea* (N.S.) **9** pp. 145–229.

PHILLIPS, J. S. (1940). Immature nutfall of coconuts in the Solomon Islands.—*Bull. ent. Res.* **31** pp. 295–316.

PHILLIPS, J. S. (1941). A search for parasites of Dasynine bugs in the Netherlands Indies.—*Trans. R. ent. Soc. Lond.* **91** pp. 119–144.

PHILLIPS, J. S. (1956). Immature nutfall of coconuts in the British Solomon Islands Protectorate.—*Bull. ent. Res.* **47** pp. 575–595.

VANDERPLANK, F. L. (1958). Studies on the coconut pest, *Pseudotheraptus wayi* Brown (Coreidae), in Zanzibar. I. A method of assessing the damage caused by the insect.—*Bull. ent. Res.* **49** pp. 559–584.

© Commonwealth Agricultural Bureaux, 1959.



FIG. 1. Extending ladder used for investigations in coconut palms.



FIG. 2. Egg of *Amblypelta cocophaga cocophaga* China 10 the basal recess of the underside of a leaflet of a coconut frond.



FIG. 3. Egg of *Amblypelta cocophaga cocophaga* on stem of cassava (*Manihot esculenta* Crantz).



FIG. 4. Two eggs of *Amblypelta cocophaga cocophaga* laid on the back of another insect of the same species in captivity.

THE YIELD RESPONSE OF COTTON IN THE SUDAN GEZIRA TO DDT SPRAY.

By R. J. V. Joyce *

Research Division, Ministry of Agriculture, Wad Medani, Sudan.

Contents.

PAGE

Yields of sprayed and unsprayed cotton 569
Method of sampling for appraisal of spraying 569
Summary of results 569
Validity of the data 571
Causes of seasonal variation in response to spraying 573
Discussion of observed variations in response to spraying 576
Experimental study of interaction of factors affecting yield 576
Experimental layout and methods 576
Results: insect populations and cotton yields 578
Varietal difference in the yield response to spraying 589
Discussion 591
Summary 593
Acknowledgements 594
References 594

In the Sudan Gezira, where some 240,000 feddans † of cotton are grown by irrigation water supplied by gravity from the Sennar Dam, the application of DDT to the crop in sprays was introduced during the season 1945–46, with the experiments reported by Cowland & Edwards (1949). The apparent yield benefit encouraged the adoption of the practice on an increasing scale. At the same time, nitrogenous fertiliser, whose importance to cotton yields in the Gezira had been established by Crowther (1934, 1941, 1944), became available after the war and was likewise applied on an ever increasing scale. The yield improvements that followed the introduction of these two new practices were smaller than expected. The yield response of cotton to DDT spray apparently fluctuated greatly from year to year and place to place. It was hoped that by examining the causes of these fluctuations it would be possible to appraise the value of DDT spraying and to predict during what season and at what places it would be profitable.

---

* Now with Desert Locust Survey, Nairobi, Kenya.

† In this communication the following local terms are employed:—

1 feddan = 1·038 acres = 0·42 hectares.

1 kantar (cotton) = 315 rotls (312 lb.) of seed cotton, yielding approximately 100 lb. of lint of Domains Sakel and 107 lb. of lint of X1730A.

1 rotl = 0·9905 lb. = ·4494 kg.

Yields are expressed in kantars per feddan (k.p.f.).

TABLE I.

Yield differences between selected sprayed and unsprayed cotton Numbers (90-feddan fields) in the Sudan Gezira.

Expressed as excess yield from sprayed cotton (in k.p.f.).

Group	*1949–50*	*1950–51*	*1951–52*	*1952–53*	*1953–54*	*1954–55*	*1955–56*	*1956–57*	Mean
South	—	− 0·23	1·64	0·06	0·39	1·01	0·17	− 0·10	0·42
Centre	1·39	− 0·27	0·68	0·62	− 0·11	0·93	0·69	0·19	0·51
Messellemiya	0·92	0·95	0·96	1·22	0·74	0·76	0·16	0·27	0·75
West	2·50	0·21	0·80	0·90	1·01	1·54	0·63	0·77	1·04
North	2·11	1·70	1·07	1·00	1·25	1·04	0·73	1·32	1·28
Northwest	—	—	—	—	—	0·77	1·79	1·72	1·43
Mean*	1·73	0·47	1·03	0·76	0·66	1·01	0·70	0·70	—
S.E. (Treatment mean)	±0·25	±0·27	±0·12	±0·14	±0·17	±0·11	± 0·17	±0·20	
L.S.D. ($P = 0·05$)	1·13	*N.S.*	0·48	0·56	0·66	0·39	0·62	0·74	
($P = 0·01$)	—	—	0·80	—	—	0·62	—	—	

— represents no experiment conducted.

S.E. = Standard error. L.S.D. = Least significant difference of a response.

N.S. = Not significant.

* The mean values plotted in figs. 1, 3 and 4 have been adjusted for the missing value for South Group in 1949–50, and by averaging the values for North and Northwest Groups in 1954–57.

Yields of Sprayed and Unsprayed cotton.

DDT is applied to cotton in the Gezira to kill the cotton jassid, *Empoasca lybica* (de Berg.). It is applied in a spray in October, when the crop is 6–10 weeks old and when infestations are low and little hopper-burn apparent. If spraying is delayed until visual damage is conspicuous, the response is reduced, and Snow & Taylor (1952) were able to establish a regression of Gezira cotton yields on date of spraying, which indicated a loss that varied, in different seasons, from 0·16 to 0·41 kantar per feddan (k.p.f.) for every ten days' delay in spraying date during October and November. DDT spray, while it may initially reduce infestations of cotton whitefly, *Bemisia tabaci* (Gennadius), is followed by a population resurgence that causes no obvious damage until December, when it may be associated with severe contamination of the plant by honeydew.

Method of Sampling for Appraisal of Spraying.

Unsprayed cotton in the Gezira is apt to be severely damaged by hopper-burn, and experiments requiring unsprayed cotton were therefore resisted by the tenants, who, as partners in the Sudan Gezira Board, contributed to the cost of spray whether their own cotton was treated or not.

In 1949, however, the Gezira Board selected in each of the 40 (now 44) administrative Blocks into which the scheme is divided, two 90-feddan cotton fields or Numbers (a 'Number' constituting the unit of the 8-course rotation). Both Numbers had to be typical of the Block and at a similar stage of growth, with the same mean sowing date, the same fertiliser treatment, and being of the same phase in the rotation. One of the Numbers was subsequently sprayed with DDT and the other unsprayed.

Because bias in choice of Numbers was suspected, the system was changed in 1952–53 so that Group Inspectors (those in charge of several Blocks) made the selection within the same limitations. There were obvious statistical objections to this method of choice and in 1955–56 the Board accepted the advice of the Research Division Statistician, who had investigated the variability in yield of Gezira cotton Numbers, and agreed to select at random in each Block two neighbouring (but not adjoining) cotton Numbers, watered by the same canal, and to apply sprayed and unsprayed treatments at random to them. The variability of pairs selected in this way was less than that of pairs of Numbers chosen completely at random and equalled the variability of pairs chosen by the method previously employed.

Summary of Results.

To determine mean seasonal response, the yields of selected sprayed and unsprayed Numbers were bulked together into Groups,* which were regarded as replicates of an experiment comparing two treatments, one sprayed and the other unsprayed. The results are summarised in Table I.

A mean response to spraying over eight seasons was calculated by bulking the figures for North and Northwest Groups for the three seasons for which both were available, and by computing the figures for South Group, 1949–50, from a formula for missing plots. With these adjustments a mean response to spray of 0·816 $\pm$ 0·12 k.p.f. was obtained. The least significant differences for comparing the yield of selected sprayed and unsprayed Numbers were 0·48 k.p.f. (for $P = 0{\cdot}05$) and 0·80 k.p.f. (for $P = 0{\cdot}01$).

* 'Groups' are administrative areas consisting of 5–10 Blocks and cropped with 34,000–43,000 feddans of cotton. There are six such Groups: South, Centre, Messellemiya, West, North and Northwest. Messellemiya and West Groups cover approximately the same latitudes, but apart from this the order in which the Groups are arranged in the tables in this paper is geographical, from south to north.

TABLE II.

Group mean yields (k.p.f.) of some sprayed and unsprayed comparison Numbers.

Group	Seasons							
	1949–50		*1954–55*		*1951–52*		*1954–55*	
	Sprayed in 1954–55	Unsprayed in 1954–55	Sprayed	Unsprayed	Sprayed in 1954–55	Unsprayed in 1954–55	Sprayed	Unsprayed
South	3·99	4·86	5·05	4·79	1·16	1·85	5·38	2·33
Centre	3·20	3·39	4·60	3·44	3·20	2·78	2·58	2·45
Messellemiya	5·50	5·46	4·25	3·65	4·23	3·98	3·50	3·09
West	3·66	4·82	3·94	3·42	3·48	3·65	4·57	2·32
North	4·85	4·07	3·65	2·98	3·30	3·72	4·65	3·38
Mean	4·24	4·52	4·30	3·66	3·07	3·20	4·14	2·71
S.E. (treatment mean) ..	±0·137		±0·100		±0·148		±0·387	
Least significant difference ($P = 0·05$)	Difference not significant		0·39		Difference not significant		Difference not significant	

1949–50, 1951–52: Same treatment applied to both members of each pair of Numbers.

1954–55: Sprayed treatment applied to one member of each pair of Numbers.

Validity of the Data.

In order to assert that the data derived from the sample Numbers described the yield response to DDT spray in the Gezira as a whole, it is necessary to demonstrate the validity of three assumptions:—

(i) that the sample was effectively random;

(ii) that the 90-feddan unsprayed Numbers, situated in an environment of sprayed cotton, behaved in respect of yield as they would have done had their environments been unsprayed;

(iii) that the samples of sprayed and unsprayed cotton were representative of the Gezira as a whole.

The first assumption is impossible to prove. It is likely to be valid, because it would be difficult even for a biased Inspector to choose, 4–6 weeks after sowing, cotton typical of his Block that would yield, seven months later, more, or less, cotton than that chosen for comparison and subsequently sprayed. Moreover, the results obtained during 1955–56 and 1956–57, when a purely random method of choice was adopted, were not much dissimilar from those of earlier seasons.

Nevertheless, in order to detect the possible effect of bias on the results, an investigation was made of the Numbers chosen during 1954–55 and 1955–56 in respect of their yields when last previously cropped with cotton. Any yield differences at those times, when both members of each pair had been similarly treated in respect of spray, would indicate inherently different soil fertilities or standards of cultivation.

During the 1954–55 season, 27 pairs of comparison Numbers had been cropped previously, seven pairs during 1949–50 and seven during 1951–52 seasons. In the remaining 13 pairs, one of each pair was cropped in 1949–50 and the other in 1951–52 season, *i.e.*, one of the limitations in random selection, namely that both Numbers should be of the same phase in rotation, had not been observed. The yields of the Numbers during the 1954–55 season, when spray treatments were applied to one member of each pair of Numbers, and during their previous season of cropping, when neither member, or else both members, of each pair was sprayed, are summarised in Table II.

In 1949–50 and 1951–52, when spray treatments were identical for both

TABLE III.

Group mean yields (k.p.f.) of sprayed and unsprayed Numbers.

Group	Yields in 1952–53		Yields in 1955–56	
	Sprayed in 1955–56	Unsprayed in 1955–56	Sprayed	Unsprayed
South	4·48	4·22	6·26	5·55
Centre	4·34	4·32	5·49	4·08
Messellemiya ..	4·46	4·43	4·56	4·95
West	5·17	4·79	3·98	3·01
North	6·25	5·85	4·32	3·85
Northwest ..	5·53	4·02	5·89	3·26
Mean	5·04	4·67	5·08	4·12
S.E. (treatment mean)	±0·12		±0·29	
Least significant difference ..	Not significant		1·05	

1952–53 Spray treatment the same for both members of each pair.
1955–56 Spray treatments applied to one member of each pair.

members of each pair, the comparison Numbers cropped similarly, and the small differences which occurred could be attributed to chance. In 1954–55, the application of treatments to these same Numbers was followed by significantly (or nearly significantly) greater yields from sprayed than from unsprayed treatments.

In 1955–56, 19 of the randomly selected pairs of Numbers had been cropped previously with cotton, during 1952–53. The yields during the two seasons are summarised in Table III.

It is apparent that where yield differences (which were not significant) existed during 1952–53, these were increased when spray treatments were applied during 1955–56, although the yield difference just failed to reach significance at $P = 0{\cdot}05$.

This investigation does not support the view that bias in selection of the samples to be sprayed measurably affected the results.

With regard to assumption (ii), a special experiment was conducted to investigate what size of plot it was necessary to use in the Gezira, for an experiment testing the effect of insecticides on cotton pests, so as to ensure that the unsprayed plot behaved independently of its differently treated neighbour. The results of this experiment are reported elsewhere (Joyce & Roberts, 1959); it provided no evidence that a 90-feddan plot of unsprayed cotton would behave differently in an unsprayed, compared with a sprayed environment, so that assumption (ii) can be provisionally accepted.

TABLE IV.

Yield of selected sprayed Numbers and Group mean yields (k.p.f.).

Means over 5 Groups

Season	Selected sprayed Numbers	Group average
1949–50	5·41	4·59
1950–51	7·26	6·80
1951–52	3·33	2·97
1952–53	4·54	4·66
1953–54	4·92	4·75
1954–55	4·42	4·28
1955–56	5·10	4·95
1956–57	6·90	6·84
Mean ..	5·23	4·98

Means over all seasons

Group	Selected sprayed Numbers	Group average
South ..	5·64	5·34
Centre ..	5·17	4·91
Messellemiya ..	4·85	4·81
West ..	5·07	5·02
Northwest ..	5·41	4·82
Mean ..	5·23	4·98

S.E. (over-all mean)	±0·071
Least significant difference ($P = 0{\cdot}05$)	0·24
S.E. (horizontal comparisons)	±0·16
S.E. (other comparisons)	±0·20

With regard to assumption (iii), the size of the sample of sprayed and unsprayed cotton represented just over three per cent. of the total area cropped with cotton. Since, during the period under consideration, nearly all the cotton in the Gezira was sprayed, the yields of the selected sprayed Numbers should be similar to those of the Gezira as a whole if the sample were adequate in size. Accordingly, an analysis of variance was made of the yields of the selected Numbers and those of the Group to which they belonged. These are given in Table IV.

The conclusion that may be drawn from these data is that there was an average bias in the selected sprayed Numbers of + 0·25 k.p.f. (± 0·071) and that this bias did not change systematically according to Groups or seasons.

The regression equation connecting the mean yields of the selected sprayed Numbers and those of the corresponding Groups was also investigated. This was:—

$$Y = 0{\cdot}38 + 0{\cdot}879x \ (\pm\ 0{\cdot}064)$$

Where Y is the Group mean yield (k.p.f.) and x is the yield of selected sprayed Number (k.p.f.). The figure in brackets is the standard error of the regression coefficient.* It will be seen that the regression coefficient just fails to be significantly less than unity.

The bias in favour of x is given by:—

$$x - Y = 0{\cdot}121x - 0{\cdot}38$$

Thus x will equal Y only if $x = 3{\cdot}140$ k.p.f.; if it is greater it will exceed Y. That is, whereas bias was shown not to vary systematically according to seasons and Groups it did vary according to level of yield.

The regression coefficient of Y on x after eliminating seasonal differences was:—

$$0{\cdot}495 \ (\pm\ 0{\cdot}101)$$

which is highly significantly less than unity. This may be partly ascribed to the fact that x is more variable than Y, but it may also be due to the variability of the original subjective choice of cotton Numbers supposedly typical of the Blocks.

It is concluded that the samples of sprayed cotton, although tending to be biased towards better-than-average cotton, and therefore not ideal, gave a reasonable estimate of the behaviour of sprayed cotton in the Gezira. It seemed worth while, therefore, to accept the validity of the three assumptions and to proceed further with the analysis.

Causes of Seasonal Variation in Response to Spraying.

It was previously known that part of the variation in response to spray from season to season might possibly be explained by a number of factors. Those investigated were: a trend with time; the rain in the pre-sowing period; the recorded infestation by nymphs of *E. lybica*; the use of nitrogenous fertiliser; and the variety of cotton grown.

Trend in time.

Linear trends, in time, of spraying effect were examined by denoting seasons as t, which took the values 1, 2, ... 8, corresponding to the eight seasons (1949–50 to 1956–57) considered. The regression coefficient of response to spray on time was − 0·0729 (± 0·048) k.p.f. per year, and this was not significant.

---

* In this and other regression equations in this paper, the standard error of the regression coefficient is given in brackets at the end of the equation.

Pre-sowing rains.

This rain, defined as that falling between 1st July and 15th August, is correlated positively with Gezira cotton yields (Crowther, 1941) and has been shown by Joyce (unpublished) to be negatively correlated with infestations of *E. lybica*. When the 40 pairs of results (5 Groups × 8 seasons) were considered, the correlation of yield response with pre-sowing rains ($r = -0{\cdot}4617$, for 38 degrees of freedom), was significant at $P = 0{\cdot}01$. The regression equation of yield response on pre-sowing rains was:

$$Y = 1{\cdot}46 - 0{\cdot}00401x_1 \ (\pm\ 0{\cdot}00125) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ (1)$$

where Y is the yield response to spray (expressed as kantars seed cotton per feddan), and x_1 represents pre-sowing rains (in mm.). The figure in brackets is the S.E. of the regression coefficient. After eliminating seasonal and site effects, the regression coefficient of the residual variance:

$$b \text{ (residual)} = 0{\cdot}00190 \ (\pm\ 0{\cdot}0026)$$

was not significant, but the covariance of Group (*i.e.*, site) and seasonal pre-sowing rains and yield effects were significant. That is to say, the correlation between pre-sowing rains and yield response was probably due to factors which varied between Groups and seasons but were correlated with these rains.

The regression of yield response to spray on rainfall in July only (x_1'') was also investigated. The regression coefficients were as follows:—

Source of covariance	d.f.	Regression coefficient b
Groups	3	− 0·0231 (±0·0126) N.S.
Seasons	6	− 0·0036 (±0·021) N.S.
Error	27	− 0·0177 (±0·0031) +++
Total	38	− 0·0057 (±0·0016) +++

N.S. Not significant
+++ Significant ($P = 0{\cdot}001$)

from which the regression equation:—

$$Y = 2{\cdot}465 - 0{\cdot}0177x_1'' \ (\pm\ 0{\cdot}0031) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ (2)$$

may be derived, where x_1'' represents the July rainfall in mm., and Y is as before.

When the mean seasonal response to spraying computed from this equation was plotted against the actual responses (fig. 1), it was apparent that the deviations of computed from actual responses were very great. Accordingly, the difference between regression coefficients derived from site and seasonal covariance was examined. The regression coefficient describing the seasonal effect of factors correlated with July rainfall on response to spray differed significantly from that derived from the residual covariance, which is probably related to the direct effect of these rains on spray response. That is to say, after adjusting yield response to July rainfall in accordance with equation (2), significant seasonal differences in response still existed. Similarly, although the regression coefficient derived from the site covariance did not differ significantly from that derived from the residual covariance, significant differences still existed between Groups after the yield response had been adjusted for July rainfall.

The analysis thus proves that while yield response to DDT spraying is significantly correlated with July rainfall, other factors, associated with site and season

and also correlated with this rainfall, cause significant deviations from the expected yield response. That is to say, the response to spray differs in different seasons and different places to a greater extent than would be expected from examination of the July rainfall alone.

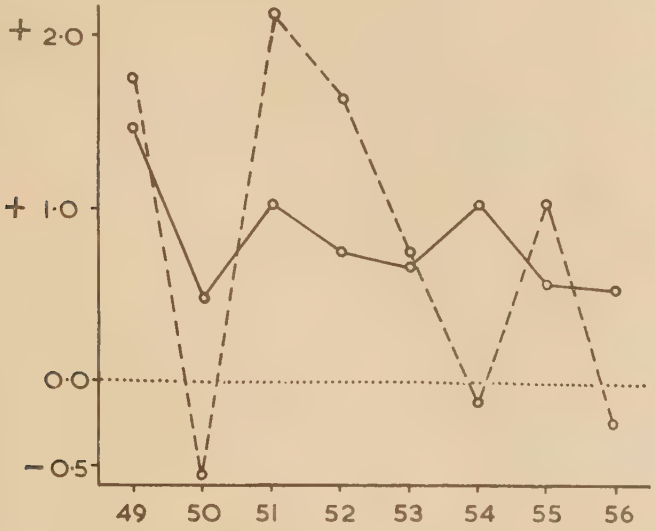


Fig. 1.—Mean increase in yield of cotton due to spraying, Sudan Gezira, 1949–56. Actual increase from sample areas (data from Table I, p. 568), solid line; increase computed from regression equation (2), p. 576, broken line. Abscissae: year of sowing. Ordinates: kantars per feddan.

Infestations of cotton jassid.

The records of jassid infestations do not represent an accurate sample, but are considered to show only general seasonal trends in Sudan Gezira Board Groups (Joyce, unpublished). They were irregular assessments, sometimes made only at a time judged to coincide with peak infestation, and they were not necessarily taken from the same unsprayed cotton as that used in yield measurement. Accordingly, any relation between the jassid infestations and yield response may be fortuitous or, on the other hand, may indicate that an even better relationship could be established with more precise data on jassid infestations.

Since insect assessment had to be grouped into four geographical areas, approximating to the South, Centre, Messellemiya, and North plus Northwest Groups, the regression of yield response to spraying on the recorded insect infestation could be analysed only in relation to those Groups, West Group being omitted.

When the 32 pairs of results (4 sites × 8 seasons) were considered, the regression of yield response on peak jassid infestation failed to reach significance at $P = 0{\cdot}05$. The formula for the regression was:

$$Y = 0{\cdot}557\ x_3\ (\pm\ 0{\cdot}356) - 0{\cdot}556 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ (3)$$

where x_3 represents the logarithm of the peak infestation of nymphs of *E. lybica* per 100 leaves, and Y is as before.

Application of nitrogenous fertiliser.

An analysis was made of the regression of the Group yield response to spray with the mean amount of nitrogenous fertiliser applied each season. The regression was significant, but absence of correlation in the residual covariance suggested that the effect of the fertiliser might not be direct.

Variety of cotton.

The increase in the response to spraying that is apparent in the mean figures in Table I, progressing from South Group (0·42 k.p.f.) to Northwest Group (1·43 k.p.f.) may be a site effect due to differences in geographic situation. On the other hand, because South and Centre Groups grow only X1730 cotton, North and Northwest Groups only Domains Sakel, and West and Messellemiya a mixture of these two varieties, it may equally be a site difference due to variety. The data did not allow of further analysis of these factors.

Discussion of observed Variations in Response to Spraying.

The important conclusion from this analysis is that pre-sowing rains, particularly those falling in July, influenced the response of cotton in the Gezira to DDT spray. There were, however, seasonal and site factors that were also correlated with these rains and significantly and strikingly changed the relationship. There was some suggestion that time trends, infestations of *E. lybica*, application of nitrogenous fertiliser, and variety of cotton all affected the seasonal response to spray. On examination, all these factors were found to be related to pre-sowing rains: *E. lybica* because of the effect of these rains and of nitrogenous fertiliser on its subsequent rate of breeding (Joyce, unpublished); variety because of the policy of growing X1730 in heavy- and Domains Sakel in light-rainfall areas; and nitrogenous fertiliser because, by chance, both the rate of application of nitrogen and the intensity of pre-sowing rains tended to increase over the period examined (r, for nitrogen on pre-sowing rains = 0·4657, which, for 21 degrees of freedom, is significant at $P = 0·05$).

Experimental Study of Interaction of Factors affecting Yield.

In order to obtain a more precise measure of the effect of nitrogenous fertiliser, cotton variety and insect infestations on the response of cotton to DDT spray, the following series of experiments was conducted in 1956–57.

Experimental Layout and Methods.

In order to discover how the three factors affected yield in different parts of the Gezira, a complete experiment was conducted in each of the Groups into which the Gezira is divided.* For convenience of spraying, a split-plot design was chosen, each main treatment (spray *v.* no spray) being applied to a single 90-feddan cotton Number, containing nine 10-feddan tenancies designated A, B, etc. Each sub-treatment, consisting of one of two levels of application of nitrogen, or of none, was applied at random to one of three groups, each of three tenancies, *i.e.*, A, B, C; D, E, F; and G, H, I. The whole was replicated ten times in each Group, thus using 20 Numbers or 1,800 feddans of cotton. The experiment was repeated in all but the South Group.

The treatments shown in Table V were applied.

The spray treatments consisted of 0·75 lb. technical DDT per feddan applied in one of three methods:—

(i) Low volume (LV) spray, applied as 10 gal. emulsion per feddan at a

* See footnote, p. 569.

pressure of 40 lb. per sq. inch by means of a 30-ft. spray-bar fitted with two wide-angle nozzles travelling above the crop and spraying downwards;

(ii) High volume (HV) spray, applied as 25 gal. emulsion per feddan at 40 lb. per sq. inch by means of a 30-ft. spray-bar fitted with ten wide-angle pendant nozzles travelling below the top of the crop and spraying upwards;

(iii) ultra low-volume spray, applied as 2 gal. emulsion per feddan by means of rotary atomiser fitted to the wingtips of a Tiger Moth or Auster J.5.G. aircraft.

TABLE V

Sub-treatment (Level of nitrogen)	Main treatment	
	Sprayed	Unsprayed
N_0 ..	1	2
N_1 ..	3	4
N_2 ..	5	6

N_0 = Nil
N_1 = 45 rotls nitrogen per feddan (as urea)
N_2 = 90 ,, ,, ,, ,, ,, ,,

The spraying dates were between 1st to 15th October 1956. The varieties and methods of application used in the different Groups are shown in Table VI.

TABLE VI

Group	Variety	Spray method
Northwest ..	Domains Sakel	Air
North	Domains Sakel	HV
West	Domains Sakel	Air
	X1730A	HV
Messellemiya ..	Domains Sakel	HV
	X1730A	HV
Centre	X1730A	LV
	BAR XLI	HV

The yield was assessed in all Groups. The effect of the treatments on insects was assessed only in the Centre and Northwest Groups; in each of these, insects were counted in the central tenancies of each sub-treatment, namely B, E, and H, from each of six replicates chosen at random. Counts were made, at inter-watering intervals, of the numbers of adults of *Bemisia tabaci* on 500 leaves from 100 plant holes selected at random in a traverse across the tenancy, and of the number of nymphs of *E. lybica* and the number of leaves infested by larvae of thrips (*Caliothrips* spp.) on a similar sample selected in the same way. Damage due to bollworms (*Earias insulana* (Boisd.), *Heliothis armigera* (Hb.) and *Platyedra gossypiella* (Saund.)) was assessed by examining in the laboratory the fruit stripped from 20 plants selected afresh and at random from each tenancy at fortnightly intervals.

Results: Insect Populations and Cotton Yields.

Populations of cotton jassid.

Examination of the results in the Northwest Group showed the need for a logarithmic transformation of the records of populations of *E. lybica*. The results are given in Table VII.

TABLE VII.

Populations of jassids (Northwest Group).
Mean number of nymphs of *E. lybica* (expressed logarithmically) per 100 leaves in 7 counts (25.ix–20.xii.56).

	Sprayed	Unsprayed	Mean
N_0 ..	0·456	0·586	0·521
N_1 ..	0·402	0·588	0·495
N_2 ..	0·463	0·589	0·526
Mean ..	0·440	0·588	0·514

	S.E.	Least significant difference $P=0·05$	Least significant difference $P=0·01$
Spray-treatment means	±·003	·009	·012
Fertiliser-treatment means	±·003	·009	·012
Within spray treatments	±·004	·012	·017
Between spray treatments	±·005	·013	·017

The difference in infestation on sprayed and unsprayed treatments was significant at all levels of probability. The only other differences to reach significance were those on sprayed cotton, in which the infestations were significantly less on N_1 than on N_0 or N_2; there was no significant difference between the fertiliser treatments on the unsprayed cotton.

In Centre Group the assessments were analysed without a logarithmic transformation (see Table VIII).

TABLE VIII.

Populations of jassids (Centre Group).
Mean number of nymphs of *E. lybica* (expressed logarithmically) per 100 leaves in 6 counts (1.x–20.xii.56).

	Sprayed	Unsprayed	Mean
N_0 ..	16·9	117·6	67·2
N_1 ..	19·2	141·0	80·1
N_2 ..	23·0	181·8	102·4
Mean	19·7	146·8	83·2

	S.E.	Least significant difference $P=0·05$	Least significant difference $P=0·01$
Spray-treatment means	±3·5	10·1	13·6
Fertiliser-treatment means	±4·2	11·8	15·6
Within spray treatments	±6·0	16·7	—
Between spray treatments	±6·0	17·9	24·8

There was a marked tendency for infestation to increase with level of nitrogenous fertiliser, particularly on unsprayed cotton.

Populations of cotton whitefly.

The assessments for Northwest Group were transformed to logs, and analysis of variance of counts on eight occasions, including two pre-spray and six post-spray dates, gave the means shown in Table IX.

TABLE IX.

Populations of whitefly (Northwest Group).
Mean number of adults of *B. tabaci* per 100 leaves in 8 counts (27.ix.56–4.i.57).

	Sprayed	Unsprayed	Mean
N_0 ..	0·571	0·547	0·559
N_1 ..	0·558	0·540	0·549
N_2 ..	0·583	0·543	0·563
Mean	0·571	0·543	0·557

	S.E.	Least significant difference $P=0·05$	Least significant difference $P=0·01$
Spray-treatment means	±·0012	·004	·005
Fertiliser-treatment means	±·0007	·002	·003
Within spray treatments	±·0011	·003	·004
Between spray treatments	±·0070	·022	—

The difference in infestation on sprayed and unsprayed cotton, although small, was highly significant at all levels of fertiliser. The only other difference was that N_1 fertiliser apparently reduced, and N_2 increased, infestations.

Population records in Centre Group are given in Table X.

TABLE X.

Populations of whitefly (Centre Group).
Mean number of adults of *B. tabaci* per 100 leaves in 6 counts (1.x.56–4.i.57).

	Sprayed	Unsprayed	Mean
N_0 ..	128	51	90
N_1 ..	130	68	99
N_2 ..	191	65	128
Mean ..	150	61	106

	S.E.	Least significant difference $P=0·05$	Least significant difference $P=0·01$
Spray-treatment means	± 7	19	25
Fertiliser-treatment means	±10	28	—
Within spray treatments	±13	38	—
Between spray treatments	±14	40	—

The principal differences were those between sprayed and unsprayed cotton.

Populations of bollworms.

In Northwest Group, bollworm infestation was light. In eight samples, taken between early November and late February, all the fruit on 5,760 plants was examined and a total of 521 living bollworm larvae recovered (372 of *E. insulana*, 26 of *H. armigera* and 123 of *P. gossypiella*). Of the 26 larvae of *H. armigera*, 22 were recovered during November and early December and 17 of these from sprayed cotton. In the Centre Group, only 14 larvae of *H. armigera* were recorded in the fruit of 5,760 cotton plants examined between November and February, seven from sprayed and seven from unsprayed cotton, and all of these in November and December. In both areas *H. armigera* attacked buds and young bolls exclusively.

E. insulana was more abundant and was present in the crop from November (in buds and young bolls) to February (chiefly in mature bolls). The numbers of larvae recorded in November–February, inclusive, are shown in Table XI.

TABLE XI.

Populations of *Earias*.

Mean number of larvae of *E. insulana* per 100 plants, November–February.

	Northwest Group			Centre Group		
	Sprayed	Unsprayed	Mean	Sprayed	Unsprayed	Mean
N_0	4·17	8·75	6·46	0·31	0·62	0·46
N_1	4·69	8·02	6·35	0·52	0·31	0·41
N_2	5·00	8·12	6·56	0·21	0·52	0·36
Mean ..	4·62	8·29	6·45	0·34	0·48	0·41

Infestations were considerably heavier in Northwest than in Centre Group and, at the former site, on unsprayed than on sprayed cotton. The variances were not calculated, but the data showed that the difference was due to higher infestations in January–February only, related to the greater number of bolls present on unsprayed cotton at this date. In contrast, during November and early December *E. insulana* tended to be more numerous on sprayed than on unsprayed cotton.

P. gossypiella was recorded only after late December. Infestations were low, particularly in the Centre Group, and were not apparently affected by treatments (Table XII).

TABLE XII.

Population of *Platyedra*.

Mean number of larvae recorded per 100 plants during December.

	Northwest Group			Centre Group		
	Sprayed	Unsprayed	Mean	Sprayed	Unsprayed	Mean
N_0	2·19	2·29	2·24	0·83	1·35	1·09
N_1	2·92	2·39	2·65	1·56	1·35	1·45
N_2	1·46	1·56	1·51	0·62	1·01	0·81

The damage caused to mature bolls by these low bollworm populations did not apparently affect the yield of seed cotton, so it was decided to examine the damage to immature fruiting bodies during November, when this seemed to be higher on sprayed than on unsprayed cotton. Such damage, resulting in shedding, was due to both *Heliothis* and *Earias*. No attempt was made to distinguish between the damage by these two species, although the latter, being the more abundant, probably caused more loss. Bollworm damage to buds and young bolls was very light, particularly in the Centre Group, and although more damage was recorded in sprayed than in unsprayed cotton, the difference was not significant (Table XIII).

TABLE XIII.

Interaction of spraying and nitrogenous fertiliser Numbers (per 100 plants) of bollworm-damaged flower buds and young bolls recorded on the plant between 1st November and 15th December.

	Northwest Group			Centre Group		
	Sprayed	Unsprayed	Mean	Sprayed	Unsprayed	Mean
N_0	14·67	5·67	10·17	0·84	0·30	0·57
N_1	9·33	7·00	8·16	2·28	0·84	1·56
N_2	8·67	8·67	8·67	1·98	1·80	1·89
Mean ..	10·89	7·11	9·00	1·70	0·98	1·34

Yield.

The yields from each Group were analysed separately and the variances in both main and sub-plots found to be remarkably similar. Accordingly the five individual experiments were pooled to obtain common estimates of error. The mean yields are summarised in Table XIV and the responses to spraying and fertiliser in Table XV.

The response to successive increments of nitrogen was significant in all but three cases.

In the X1730A Blocks (Centre Group), unsprayed cotton gave a better response to fertiliser than did sprayed cotton, and response to spraying was significantly reduced by fertiliser.

To investigate whether these different interactions to spraying and fertiliser were a site or variety effect, the yields of Messellemiya and West Groups were considered further, for in these Groups half the experiment was sown to X1730A and half to Domains Sakel. The mean yields of each variety (over both Groups) are given in Table XVI.

Although, strictly, differences in varietal response cannot be compared since site, variety and volume of spray were partly confounded, they were so striking that they were unlikely to be due entirely to chance or to site effects.* X1730A, while giving substantial yield increase in response to nitrogen, showed no benefit from spraying. In contrast, Domains Sakel benefited only slightly from nitrogen

* The cotton Numbers growing different varieties were not randomised within each Group, but all the X1730 and all the Domains Sakel tended to be grouped together for administrative convenience. The tests of significance in Table XVI are thus not strictly valid, but this was the nearest approach that could be obtained under conditions of commercial practice to a valid comparison of spraying and fertiliser effect in relation to variety. The difference thus recorded between the two varieties in response to the treatments is large and striking; whether this should be ascribed to site or to variety is a matter of opinion, but that of the author is that variety was more important than site.

TABLE XIV.

Yields of seed cotton in kantars per feddan.

	Centre			Messellemiya			West			North			Northwest		
	Sprayed	Un-sprayed	Mean	Sprayed	Un-sprayed	Mean	Sprayed	Un-sprayed	Mean	Sprayed	Un-sprayed	Mean	Sprayed	Un-sprayed	Mean
N_0 ..	5·04	4·58	4·81	5·81	4·96	3·38	5·27	4·85	5·06	5·59	3·97	4·78	6·90	5·56	6·23
N_1 ..	6·01	5·97	5·99	6·13	5·27	5·70	5·88	5·31	5·60	6·03	4·59	5·31	7·59	5·92	6·75
N_2 ..	6·92	6·80	6·86	7·01	6·31	6·67	6·65	5·18	5·91	6·39	4·99	5·69	7·16	6·09	6·63
Mean ..	5·99	5·78	5·89	6·32	5·51	5·92	5·93	5·12	5·52	6·00	4·52	5·26	7·22	5·86	6·54

	S.E.	Least significant difference $P = 0·05$	$P = 0·01$
Spray-treatment means	±0·11	0·31	0·41
Fertiliser-treatment means	±0·07	0·20	0·26
Within spray treatments	±0·10	0·28	0·37
Between spray treatments	±0·14	0·38	0·51

TABLE XV.

Interaction of spraying and nitrogenous fertiliser.

	Centre		Messellemiya		West		North		Northwest		Mean		
	Response to spraying (expressed as increased yields of seed cotton, in kantars per feddan, on sprayed plots)												
N_0	0·46		0·85		0·42		1·62		1·34		0·94		
N_1	0·04		0·86		0·57		1·44		1·67		0·92		
N_2	0·12		0·70		1·47		1·40		1·07		0·95		
Mean ..	0·21		0·81		0·81		1·48		1·36		0·93		
	Response to nitrogenous fertiliser (expressed as increases in yield of seed cotton, in kantars per feddan, over unfertilised plots, of successive levels of nitrogen)												
	S	U	S	U	S	U	S	U	S	U	S	U	Over-all mean
N_1	0·97	1·39	0·32	0·31	0·61	0·46	0·44	0·62	0·69	0·36	0·61	0·63	0·62
N_2	1·88	2·22	1·20	1·35	1·38	0·33	0·80	1·02	0·26	0·53	1·10	1·09	1·10
Mean ..	1·42	1·80	0·76	0·83	1·00	0·40	0·62	0·82	0·47	0·45	0·85	0·86	0·86

For S.E. and L.S.D., see Table XIV. S = sprayed, U = unsprayed.

in the absence of spraying, but when sprayed gave significant yield increases with increasing nitrogen.

Yield response of Domains Sakel to spraying increased significantly with the level of nitrogenous fertiliser, but in X1730A there was no interaction of spraying and fertiliser.

TABLE XVI.

Comparison of yields of X1730A and Domains Sakel (yields of seed cotton in kantars per feddan).

	X1730A			Domains Sakel			
	Sprayed	Unsprayed	Mean	Sprayed	Unsprayed	Mean	Response to spray
N_0	4·87	5·08	4·98	6·22	4·73	5·48	1·49
N_1	5·20	5·50	5·35	6·80	5·08	5·94	1·72
N_2	5·95	6·11	6·03	7·71	5·35	6·55	2·33
Mean	5·34	5·56	5·45	6·91	5·06	5·99	1·85

	S.E.	Least significant difference $P=0·05$	Least significant difference $P=0·01$
Variety means	±0·48	1·55	—
Spraying means	±0·23	0·67	0·92
Fertiliser means	±0·12	0·33	0·44
Within spray treatments	±0·16	0·46	0·62
Between spray treatments	±0·26	0·77	1·05

Response to nitrogenous fertiliser (expressed as increases in yield, in kantars per feddan, over unfertilised plots).

	X1730A			Domains Sakel		
	Sprayed	Unsprayed	Mean	Sprayed	Unsprayed	Mean
N_1 ..	0·33	0·42	0·37	0·58	0·35	0·46
N_2 ..	1·08	1·03	1·05	1·49	0·65	1·07
Mean ..	0·70	0·72	0·71	1·03	0·50	0·72

The interaction of spraying and nitrogenous fertiliser is evidently complex and is not fully explained by this series of experiments. Thus, the increased response of sprayed Domains Sakel to nitrogenous fertiliser and of fertilised Domains Sakel to spraying that was found in Messellemiya and West Groups did not occur in North and Northwest Groups. Moreover, the negative interaction of fertilised cotton to spraying that occurred in Centre Group was absent in Messellemiya and West Groups. This was reflected in the analysis as a significant second-order interaction, namely Spraying × Fertiliser × Site.

Grade.

To examine the effect on quality of the cotton crop (as measured by the official Grades into which it is classified), of spray and fertiliser treatments and

their associated differences in the incidence of pests, the yield from the experiments was divided into high grade (grades 1–4) and low grade (grades 5–9). The mean yields are summarised in this way for the Northwest Group in Table XVII.

TABLE XVII.

Yields (kantars of seed cotton per feddan) in different grades (Northwest Group, 1956–57).

	High grades (1–4)			Low grades (5–9)		
	Sprayed	Unsprayed	Mean	Sprayed	Unsprayed	Mean
N_0 ..	3·51	3·13	3·32	3·41	2·44	2·92
N_1 ..	3·55	3·48	3·52	4·04	2·44	3·24
N_2 ..	3·34	3·17	3·25	3·82	2·93	3·38
Mean ..	3·47	3·26	3·36	3·76	2·60	3·18

Data from replicates used for insect assessments.

None of the differences given in Table XVII reached significance, but whereas those in the high grades were small, the yields of low-grade cotton from the spraying and fertiliser treatments were substantially larger than those from the controls. It seems likely that the effect of spraying and fertiliser application was to increase the yields of lower-grade cotton.

Interaction of the effects of insect attack and other factors.

Possible entomological reasons for the results described in the preceding sections were investigated for Northwest and Centre Groups by analysing the covariance of the insect counts made there and the yields of the replicates from which the counts were taken. Relevant data for the Northwest Group are summarised in Table XVIII and for the Centre Group in Table XIX; the results of the analyses are discussed for the two Groups separately, those for Northwest Group below and those for Centre Group on p. 588.

Northwest Group.—The first regression investigated was that of yield on pre-spray jassid populations (those recorded on two occasions between 25th September and 9th October). The correlation was positive and significant, indicating a tendency for jassids at this early date to be more numerous on plots that eventually gave the best yields. Nitrogenous fertiliser had no effect on this tendency. When the variance due to site effects and nitrogen fertiliser was eliminated, a negative regression of yield on pre-spray jassid infestation was revealed. This could be described by the equation:—

$$Y = 14{\cdot}00 - 3{\cdot}94x_1' \ (\pm 1{\cdot}59) \quad \ldots\ldots (4)$$

where Y is the final yield in k.p.f. and x_1' is the logarithm of the mean number of jassid nymphs per 100 leaves, 25.ix–9.x.56 (in brackets is the S.E. of the regression coefficient). Thus the yield reduction caused by jassid could be predicted from the survey made at that time (25.ix–9.x).

The regression of yield on post-spray infestation of jassid populations was next examined. Post-spray jassid counts were made between 9th–17th October and 20th December–4th January. Over 41 per cent. of the total variance was accounted for by the recorded post-spray jassid infestations. When variance due to site

TABLE XVIII.

Recorded insect infestation and yields (Northwest Group, 1956–57).

Measurement		Fertiliser treatment	Sprayed	Unsprayed	Mean	Statistical tests of treatment means		
						Fertiliser	Spray	
Empoasca lybica (nymphs per 100 leaves)	Pre-spray	N_0	91	72	82 (1·88)	±0·05	±0·27	S.E.
		N_1	76	76	76 (1·86)	—	—	L.S.D.
		N_2	91	85	88 (1·93)	N.S.	N.S.	
		Mean	86 (1·89)	78 (1·88)	82 (1·89)			
	Post-spray	N_0	26	202	144 (1·82)	±0·03	±0·12	S.E.
		N_1	25	216	119 (1·78)	—	78	L.S.D.
		N_2	35	214	124 (1·86)	N.S.	++	
		Mean	29 (1·39)	211 (2·25)	119 (1·82)			
Bemisia tabaci (adults per 100 leaves)	Pre-spray	N_0	125	139	132	±0·12	±0·21	S.E.
		N_1	113	129	119	—	—	L.S.D.
		N_2	138	130	134	N.S.	N.S.	
		Mean	125	131	128			
	Post-spray	N_0	248	213	230	±0·9	±0·33	S.E.
		N_1	202	180	191	0·27	—	L.S.D.
		N_2	276	236	256	+	N.S.	
		Mean	242	210	226			
Yield (kantars seed cotton per feddan)		N_0	6·96	5·54	6·25	±0·17	±0·65	S.E.
		N_1	7·47	6·05	6·76	—	—	L.S.D.
		N_2	7·34	5·93	6·63	N.S.	N.S.	
		Mean	7·25	5·84	6·54			

S.E. Standard error
L.S.D. Least significant difference
In the case of *E. lybica*, figures in brackets refer to log transformations, to which the S.E. and L.S.D. apply.
Tests of significance: N.S. Not significant
\+ Significant at $P = 0·05$
++ Significant at $P = 0·01$

TABLE XIX.

Recorded insect infestation and yields (Centre Group, 1956–57).

Measurement		Fertiliser treatment	Sprayed	Unsprayed	Mean	Statistical tests of treatment means		
						Fertiliser	Spray	
Empoasca lybica (nymphs per 100 leaves)	Pre-spray	N_0	23	25	24	±2	±3	S.E.
		N_1	31	29	30	6	—	L.S.D.
		N_2	30	34	32	+	N.S.	
		Mean	28	29	28			
	Post-spray	N_0	12	140	76	±7	±12	S.E.
		N_1	14	167	91	23	78	L.S.D.
		N_2	18	219	119	+	++	
		Mean	15	175	95			
Bemisia tabaci (adults per 100 leaves)	Pre-spray	N_0	41	42	42	±4	±10	S.E.
		N_1	59	56	57	12	—	L.S.D.
		N_2	53	61	57	+	N.S.	
		Mean	51	53	52			
	Post-spray	N_0	177	69	123	±24	±21	S.E.
		N_1	178	90	134	—	76	L.S.D.
		N_2	237	87	162	N.S.	+	
		Mean	197	82	140			
Yield (kantars seed cotton per feddan)		N_0	4·65	4·75	4·70	±0·16	±0·43	S.E.
		N_1	6·01	5·85	5·93	0·64	—	L.S.D.
		N_2	6·67	6·86	6·77	++	N.S.	
		Mean	5·78	5·82	5·80			

Symbols and abbreviations as in Table XVIII.

and nitrogen fertiliser was eliminated, over 88 per cent. of the residual variance in final yield was found to be accounted for by post-spray infestations, the greater part of this correlation being due to the modifying effect of spray treatment on jassid infestation, the rôles played by nitrogen fertiliser and site differences being insignificant. The final equation describing the relationship between yield and post-spray jassid infestation was:—

$$Y = 9{\cdot}84 - 1{\cdot}81x_1'' \ (\pm\ 0{\cdot}51) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ (5)$$

where Y is the final yield in k.p.f. and x_1'' is the logarithm of the mean post-spray infestation of jassid nymphs per 100 leaves (in brackets is the S.E. of the regression coefficient).

Pre-spraying infestations of whitefly and of thrips were uniform throughout the experiment and no significant pre-spray differences could be detected. Yields throughout the experiment tended to be negatively correlated with post-spraying whitefly infestation, notwithstanding the fact that both spraying and fertiliser, which improved yields, also increased whitefly. When the variance from these sources was eliminated, the residual regression of total yield on whitefly infestation just reached significance at the 5 per cent. level of probability, giving the equation:—

$$Y = 7{\cdot}87 - 0{\cdot}058x_2 \ (\pm\ 0{\cdot}0027) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ (6)$$

where Y is the total yield in k.p.f. and x_2 is the mean number of adult whiteflies recorded during October and November (in brackets is the S.E. of the regression coefficient).

The regression of yield in post-spray populations of thrips, *Caliothrips* spp., could similarly be described by the equation:—

$$Y = 7{\cdot}08 - 0{\cdot}101x_3 \ (\pm\ 0{\cdot}012) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ (7)$$

where Y is the final yield in k.p.f. and x_3 is the angular transformation of the mean percentage of leaves infested by thrips larvae during October and November (in brackets is the S.E. of the regression coefficient).

The relationship is derived largely from the modifying effect of the spray treatment on infestations after eliminating the effects of nitrogen treatments and site differences.

Centre Group.—Data for the infestations and yields of the replicates on which insect counts were made in the Centre Group are given in Table XIX.

The application of nitrogen significantly increased pre-spray infestations of both jassid and whitefly, which did not differ between plots subsequently sprayed or left untreated. Correlations between pre-spray infestations and yields were not calculated. There was a positive correlation, which failed to reach significance, between yields and post-spray jassid infestation. When the variance due to the increased jassid infestation, and increased yield, following application of nitrogen was eliminated, the correlation between yield and post-spray jassid infestation was negative, but not significant. Within the spray treatments (which significantly increased whitefly numbers and tended, if anything, to reduce yields), there was a negative correlation between whitefly and yields, which was, however, not significant. The application of nitrogen, which increased yield, tended likewise to increase whitefly, but the relation failed to reach significance.

In Centre Group, therefore, there was no evidence that spraying either increased or reduced yields as a result of its effect on pests. Nitrogenous fertiliser significantly increased yields despite its tendency to increase jassid and whitefly, which in turn tended to reduce yields.

Varietal Difference in the Yield Response to Spraying.

The experiments reported above revealed an important difference in the response of the two main cotton varieties grown in the Gezira to the combined effects of nitrogenous fertiliser and spray applications of DDT. The yields of the sample fields of sprayed and unsprayed cotton were therefore re-examined separately for the two varieties concerned, X1730A and Domains Sakel. To do this, the mean yields of the samples were calculated for the different Groups in the Gezira, as follows:—

X1730A	Domains Sakel
South	Messellemiya
Centre	West
Messellemiya	North
West	Northwest

This enabled the yield of X1730A to be compared at four sites over eight seasons, and that of Domains Sakel at three sites over eight seasons (the Northwest Group not having come fully into cultivation until 1952–53).

The mean response of Domains Sakel to DDT spray (expressed as the difference in yield, in kantars seed cotton per feddan, of sprayed and unsprayed Numbers) over eight seasons is shown in Table XX.

TABLE XX.

Response of Domains Sakel to DDT Spray.

	1949	*1950*	*1951*	*1952*	*1953*	*1954*	*1955*	*1956*	Mean
Messellemiya ..	0·92	1·00	1·08	1·57	1·16	0·63	0·55	0·56	0·93
West	2·50	0·33	0·92	0·47	1·37	1·41	1·07	1·05	1·14
North	2·11	1·70	1·12	1·04	1·07	1·04	0·77	1·32	1·27
Mean	1·84	1·01	1·04	1·03	1·20	1·03	0·80	0·98	1·11

The year given is that in which the crop was sown.
S.E. Group means ±0·24 k.p.f.
S.E. seasons mean ±0·14 k.p.f.
S.E. other comparisons ±0·41 k.p.f.

There were no significant differences between individual, or between the mean Group, responses to spraying. When the mean seasonal responses to spraying are considered, the only differences reaching significance are those between 1949 and 1955 or 1956.

The regressions of spraying response on pre-sowing rain and on nitrogenous fertiliser were examined. The regression coefficient of spray response on July rains was negative, but not significant ($-0{\cdot}00133 \pm 0{\cdot}04900$). The regression coefficient of spray response on fertiliser was positive, but likewise not significant ($0{\cdot}8124 \pm 1{\cdot}524$). Either these factors exerted no effect on spray response, or else they tended to cancel each other out. Each Group received similar amounts of fertiliser throughout the period investigated, and there was a significant correlation between Group mean response and pre-sowing rains ($r = 0{\cdot}9990$ for 1 d.f.). There was a chance tendency for both fertiliser and July rains to increase with time, and the seasonal factor affecting the regression of yield response on fertiliser was negative and highly significant ($r = -0{\cdot}7375$, for 19 degrees of freedom).

It therefore seems likely that pre-sowing rains decreased yield response to spray and that nitrogenous fertiliser increased it, but that during the period considered these two effects were more or less balanced, so that the response did not change significantly from year to year.

The spray response of X1730A was examined in the same way as that for Domains Sakel. The data are not tabulated here, but consideration of the 32 comparisons (8 seasons × 4 sites) available showed the yield response to be negatively correlated with pre-sowing rains and with nitrogenous fertiliser. The partial correlation coefficients were calculated and gave the equation:—

$$Y = 1{\cdot}247 - 0{\cdot}0041x_1'' \ (\pm 0{\cdot}0020) - 0{\cdot}291x_2 \ (\pm 0{\cdot}222) \ldots\ldots\ldots\ldots (8)$$

where Y is the response to spray (in kantars per feddan), x_1'' represents July rainfall (in mm.), and x_2 represents quantity of nitrogenous fertiliser applied, of which 1 unit = 45 rotls nitrogen per feddan.

The coefficient for pre-sowing rains (x_1'') just reached significance at $P = 0{\cdot}05$; that for fertiliser (x_2) was not significant. When the actual (recorded) yield response to spray was plotted against that computed from equation (8), a close relationship was apparent (fig. 2). The variance in yield response accounted for

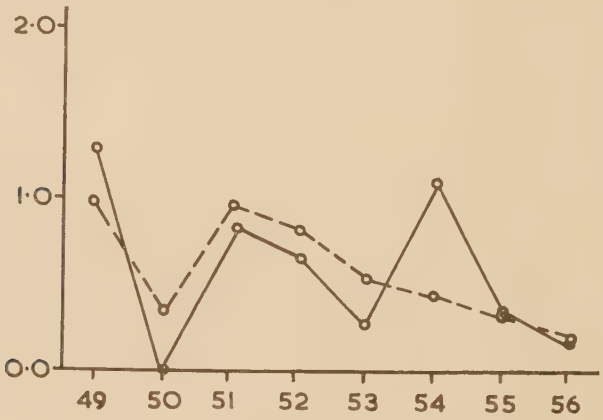


Fig. 2.—Response of cotton variety X1730A to spraying, Sudan Gezira, 1949–56. Actual increase from sample areas (see p. 568), solid line; increase computed from regression equation (8), above, broken line. Abscissae: year of sowing. Ordinates: kantars per feddan.

by July rainfall and nitrogenous fertiliser was a significant part of the total variance, and the deviation of the actual response from that computed from the regressions was not significant.

When the co-variance due to the effects of site and season was eliminated, it was found that the residual variance in yield response was not significantly correlated with rainfall or fertiliser. Moreover, while fertiliser tended to lower the yield response to spray, July rains tended to increase it; both these tendencies could, however, have been due to chance. The covariance due to seasonal factors was similar to that described for the total covariance, while site exerted very little effect on the relation of response to rains and fertiliser. That is to say, seasonal factors increased the depressing effect of fertiliser on yield response to spray and reversed significantly the tendency for July rain to improve the response.

Discussion.

It was shown earlier (pp. 573–575) that the yield response of cotton to DDT spray was highly correlated with July rains, but that the response was significantly modified by the effects of season and site. In a later section (pp. 581–584), differences in the response of the two main Gezira cotton varieties to the combined effects of DDT spray and nitrogenous fertiliser were investigated. From this it was concluded that whereas Domains Sakel tends to give an increased response to spray with increased levels of fertiliser, X1730A tends to give a reduced response in such conditions. Much of the yield benefit derived by Domains Sakel from DDT spray was shown to be due to the reduction of infestations of *E. lybica* and *Caliothrips* spp. and to occur despite increased infestations of *B. tabaci*, which were also shown to reduce yield. None of these pests apparently affected yields of X1730A in the experiments reported.

Since the policy of the Sudan Gezira Board is to grow X1730A in the higher rainfall areas of their estate, and Domains Sakel in the lower rainfall areas, a site effect, correlated with rainfall, virtually unchanging from season to season, and demonstrably affecting yield response to DDT spray, must be taken into consideration when predicting that response. This may be done by adding to regression equation (2), given on p. 574, the appropriate covariance of yield response on rainfall due to site effects.

The resultant equation was:—

$$Y = 2{\cdot}619 - 0{\cdot}019x_1'' \ (\pm\ 0{\cdot}003) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ (9)$$

the symbols used being as for equation (8).

The yield response calculated from this equation still differed significantly from the actual response, because of the significant effect, already demonstrated, of seasonal factors correlated with July rains. One of these was nitrogenous fertiliser, since, by chance, the amount of nitrogenous fertiliser applied happened to be greater in years of high pre-sowing rains. Accordingly the best equation to account for past fluctuations in yield response must include covariance due to seasonal effects. This is:—

$$Y = 1{\cdot}350 - 0{\cdot}00572x_1'' \ (\pm\ 0{\cdot}00159) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ (10)$$

the symbols used being as for equations (8) and (9). The actual responses and those computed from equation (10) are shown in fig. 3.

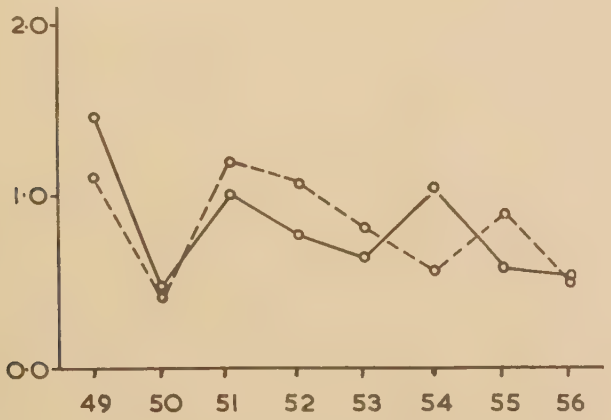


Fig. 3.—As for fig. 1, but increase computed from regression equation (10), above.

Cotton yields in the Sudan Gezira are greatly influenced by the rains falling between 1st July and 15th August. During the period 1935–36 to 1947–48, methods of cultivation remained relatively unchanged, major diseases able to depress yields were largely controlled, and no fertiliser or DDT spray was employed. The regression coefficient of Gezira yields on these pre-sowing rains was +0·0140. During the period 1949–50 to 1954–55, the regression of yields on pre-sowing rains was not significant, but the period is too short to conclude that pre-sowing rains had ceased to influence Gezira yields. However, P. Roberts (unpublished) has analysed the Gezira data for the whole period from 1935–36 to 1954–55. The regression coefficient for this more extended period is +0·00695 (±0·00274). That is to say, the effect of including six seasons when nitrogenous fertiliser was applied and spraying was practised is to reduce by about half the over-all adverse effect of a deficiency of pre-sowing rains. To explain this reduction, an examination was made of the relation between rainfall from 1st July to 15th August and response to spray, for the period for which adequate data are available (1949–50 to 1956–57). The total covariance is given in equation (1), on p. 574. When the seasonal effects are eliminated, but site effects (because of the varietal distribution of cotton in the Gezira) retained, the equation becomes:—

$$Y = 2{\cdot}026 - 0{\cdot}00753x_1 \ (\pm\ 0{\cdot}00226) \quad \text{..... (11)}$$

where x_1 represents the rainfall from 1st July to 15th August, as in equation (1), on p. 574.

That is to say, the regression coefficient describing the reduction in value of pre-sowing rains (*i.e.*, 0·0140 − 0·00695 = 0·00705) does not differ significantly from that describing the effect of pre-sowing rains on the response of cotton to DDT spraying (− 0·00753), though it is opposite in sign. Had the whole of the effect of pre-sowing rains operated through pests that were reduced by pre-sowing rains and controlled by DDT sprays, then the introduction of such sprays would have resulted in the elimination of the regression of yield on pre-sowing rains and the substitution of a regression of equal value, but opposite sign, that described the relation between these rains and the response of cotton to DDT spray. The actual responses and those computed from equation (11) are shown in fig. 4.

It seems legitimate to conclude that the widespread application of DDT sprays in recent years had reduced the deleterious effect of poor pre-sowing rains, and also that about half this effect is determined by pests that are influenced by DDT spraying.

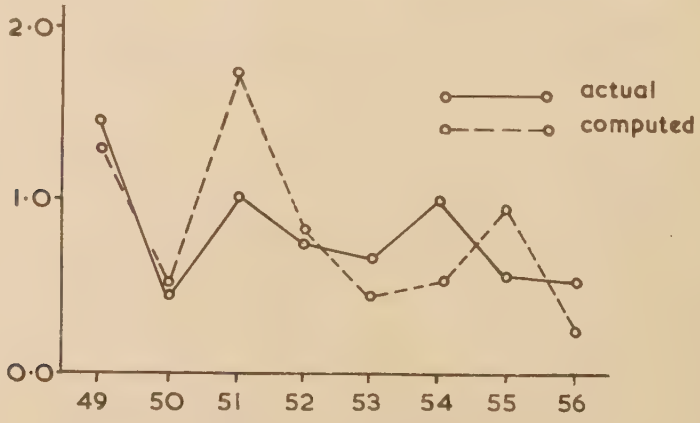


Fig. 4.—As for fig. 1, but increase computed from regression equation (11), above.

Summary.

In the Sudan Gezira, some 240,000 feddans of Egyptian-type cotton (*Gossypium barbadense*) are grown annually by gravity irrigation from the Sennar Dam, and this is sprayed with DDT, 6–10 weeks after sowing, in order to control the cotton jassid, *Empoasca lybica* (de Berg.), which is considered to reduce the yield. The seasonal yield response to DDT was estimated by comparing the yields of single sprayed and unsprayed 90-feddan fields, pairs of which were selected in each of the 40 (now 44) Blocks into which the cotton estate cropped by the Sudan Gezira Board is divided for administrative purposes. In order to establish that this estimate adequately represented that of the estate as a whole, it was necessary to show the validity of three assumptions: that the sample was representative; that the unsprayed plots, though surrounded by sprayed cotton, were sufficiently large to behave in respect of yield as if their environment had not been sprayed; and that the selection of the fields was effectively at random.

Examination of the yield history of the fields that were sprayed showed that there had been a slight bias towards the selection of fields that yielded better than the mean of the locality, and although this bias did not change from place to place or year to year, it did increase with level of yield. It is not, however, considered big enough to invalidate the first assumption.

The second assumption was tested by a special experiment reported elsewhere, which produced no evidence to suggest that a 90 feddan field would be affected in respect of yield and insect pests by proximity to a differently treated neighbouring field.

The third assumption cannot be proved, but during two seasons when fields were selected by a random procedure, the results did not differ seriously from those in years when the choice was not completely random. Moreover, when the yields of fields selected for treatment in one year were examined for the season when the fields were last cropped with cotton, and spray treatments were identical, they were found not to differ significantly, although the differences were increased and became significant in the year when sprayed and unsprayed treatments were applied.

Accordingly, the yield of the unsprayed sample is taken to indicate what the yield of the whole estate would have been had all the cotton been unsprayed.

The yield response to DDT spray of Gezira cotton, as thus estimated over the period 1949–50 to 1956–57, was shown to vary from season to season. A highly significant part of this variance was correlated with the amount of rain falling in July, some six weeks before the crop was sown, but the response was also significantly affected by both seasonal and site effects that were also correlated with this early rain. A series of experiments in 1956–57 showed that Domains Sakel cotton, which is grown in the drier, northern part of the Gezira, tended to give an increased response to DDT spray at higher levels of nitrogenous fertiliser, and that a very highly significant part of this response was due to the control of jassid, *E. lybica*, and thrips, (*Caliothrips* spp.). X1730A, grown in the wetter, southern part of the Gezira, gave no over-all response to spraying, nor was the response to nitrogenous fertiliser affected by spraying. When the yields of these varieties were examined separately over eight seasons, it was found that Domains Sakel gave a mean yield response to spraying of 1·11 kantars of seed cotton per feddan, which did not vary significantly from season to season, but that X1730A gave a yield response which was less when pre-sowing rains were good and nitrogenous fertiliser was applied. Although the regression on July rains and on fertiliser of the response of X1730A to spray failed to reach significance at $P = 0{\cdot}05$, it is considered that further data should enable a prediction of yield response of X1730A to DDT spray to be made by examination of these two factors.

Since 1935–36, yields of cotton in the Sudan Gezira have been positively correlated with the amount of rain falling between 1st July and 15th August of

the year of sowing. Comparison of the coefficient of regression of yield on this rainfall in the period (1935–36 to 1947–48) before sprays or fertiliser were applied, with that of a more extended period (1935–36 to 1954–55) including six seasons in which sprays and fertiliser were applied, shows that the latter is only about one half the former. After allowing for differences in varietal response to spraying and fertiliser, it can be shown that this decrease in the deleterious effect of a deficiency in pre-sowing rains is almost exactly accounted for by the beneficial effect of DDT spray.

It is concluded that at least half of the deleterious effect of poor pre-sowing rains on Gezira yields is a pest effect which can be eliminated by DDT spray.

The study thus provides a means whereby DDT spray may be applied selectively to those areas of the Sudan Gezira where its effect is likely to be most profitable and suggests, moreover, that such a policy would reduce the considerable seasonal fluctuations in cotton yields which in the past have characterised cropping in this area.

Acknowledgements.

I wish to express my thanks to Mr. P. Roberts, lately Statistician, Research Division, Wad Medani, who planned some of the experiments described and critically read the text of this paper, making many helpful suggestions. My thanks are also due to Sayed Mekki Abbas, formerly Managing Director, Sudan Gezira Board, for his co-operation over many years, and for his permission to use so much Board data. I am grateful also to Mr. A. M. Toms, Spraying and Experiments Officer, Sudan Gezira Board, for his never-failing help in executing the treatments of large-scale Gezira experiments, as well as to his predecessor in this post, Mr. A. Dennison. My thanks are due to the Chief of the Agricultural Research Division, Ministry of Agriculture, Sudan Government, for permission to publish this paper.

References.

Cowland, J. W. & Edwards, C. J. (1949). Control of *Empoasca lybica*, de Berg., on cotton in the Anglo-Egyptian Sudan.—*Bull. ent. Res.* **40** pp. 83–96.

Crowther, F. (1934). Studies in growth analysis of the cotton plant under irrigation in the Sudan. I. The effects of different combinations of nitrogen applications and water-supply.—*Ann. Bot., Lond.* **48** pp. 877–913.

Crowther, F. (1941). Studies in growth analysis of the cotton plant under irrigation in the Sudan. II. Seasonal variation in development and yield.—*Ann. Bot., Lond.* (N.S.) **5** pp. 509–533.

Crowther, F. (1944). Studies in growth analysis of the cotton plant under irrigation in the Sudan. III. A comparison of plant development in the Sudan Gezira and in Egypt.—*Ann. Bot., Lond.* (N.S.) **8** pp. 213–257.

Joyce, R. J. V. & Roberts, P. (1959). The determination of the size of plot suitable for cotton spraying experiments in the Sudan Gezira.—*Ann. appl. Biol.* **47** pp. 287–305.

Snow, O. W. & Taylor, J. (1952). The large-scale control of the cotton Jassid in the Gezira and White Nile areas of the Sudan.—*Bull. ent. Res.* **43** pp. 479–502.

© Commonwealth Agricultural Bureaux, 1959.

THE ECOLOGY OF *GLOSSINA LONGIPALPIS* WIED. IN SOUTHERN NIGERIA.

By W. A. Page *

Research Entomologist, West African Institute for Trypanosomiasis Research, Kaduna, Nigeria.

Contents.

	PAGE
Introduction	595
History of the investigation	595
Situation and description of the area	596
The seasons	597
Description of the investigation	598
The seasonal factor	599
Introduction	599
Comparison between the climate in the savannah and in the forest island	599
Climatic variations in the three years	599
Fly-round results when man was used as the bait	600
Results of fly-rounds using a bait-ox	606
Fly breeding	608
The food factor	608
Vegetation	610
Description of vegetational types	610
The differences in attractiveness of the various vegetational types on the man- and ox-rounds	611
The use made by *G. longipalpis* of the different types of vegetation ...	612
The trypanosome infection rate in *G. longipalpis*	612
Discussion	613
Summary	613
Acknowledgements	614
References	614
Appendix: The species of trees found in the various sections	615

Introduction.

History of the investigation.

In 1953, the West African Institute for Trypanosomiasis Research, whose entomological investigations had hitherto been carried out mainly in the dry savannah of northern Nigeria, decided to set up a small field station on the edge of the forest belt in southern Nigeria, where conditions are much more humid; by so doing, it was felt that the Institute would also obtain data applicable to the wetter parts of West Africa. After much searching, a site was chosen at Ugbobigha, a small village in Benin province, where six species of tsetse are readily found.

The investigation described below was started in November 1953 and closed in December 1956.

* Now at Dept. of Zoology, Sub-Dept. of Entomology & Parasitology, University of Edinburgh.

Situation and description of the area.

Ugbobigha (6°46′N., 6°7′E.) is situated about 60 miles NE. of Benin City, and 8 miles from Ekpoma; it is 400 ft. above sea-level. The field station is situated near the junction of the main savannah and main forest belts. To the south rises the heavily forested Ishan plateau, some 800 ft. high: to the north stretches a flat plain of black clay, which supports savannah woodland and islands of forest. It was in this plain that the investigation was carried out.

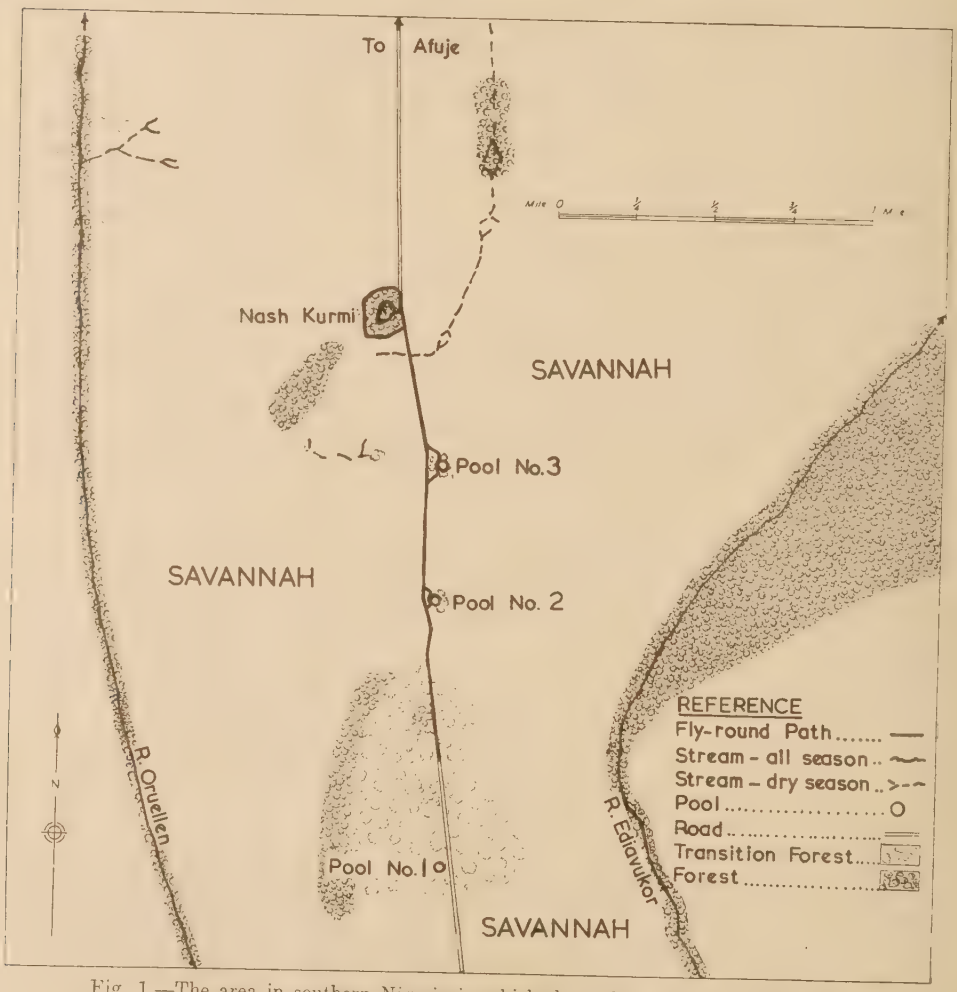


Fig. 1.—The area in southern Nigeria in which the ecology of *G. longipalpis* was investigated. The streams rise in the main forest belt, three miles to the south.

The plain is watered by two permanent streams, one to the east and one to the west (see fig. 1). In addition there are some seasonal streams, which dry up completely, and also a number of pools, remote from any streams, whose water-level and surface area vary according to the season.

The savannah is of the Southern Guinea zone type, and is probably ' derived ' savannah (Keay, 1949). The streams are lined by forests of varying width, and the pools too have their fringing vegetation. In addition, there are occasional patches of transition forest and isolated forest islands, which are not apparently associated with water. In the savannah, the coarse elephant grass grows to a height of 10 to 15 ft.; it is burnt off in January and February by the local villagers. The area itself is uninhabited, and game is plentiful.

Glossina longipalpis Wied. is ubiquitous, as is *G. palpalis* (R.-D.), which, however, occurs in much smaller numbers. *G. fusca* (Wlk.) and *G. medicorum* Aust. are found in the forest islands, and three specimens of *G. tachinoides* Westw. have been taken at the pools.

The seasons.

The year is divided into two seasons.

(*a*) *The dry season.*—The dry season lasts for four months: November, December and January are usually rainless, but in February storms are likely to occur, see Table I. The harmattan, the dry wind, which in northern Nigeria has such a profound effect on tsetse populations, is here of little importance, since it blows intermittently for only a few days; consequently, the humidity remains relatively high, as does the minimum temperature, which rarely falls below 70°F. (21°C.).

February is the hottest month of the year, when both maximum and minimum temperatures are highest, giving a mean monthly temperature of 83–84°F. (28·3—29·0°C.).

(*b*) *The wet season.*—In March and April, thunderstorms become more frequent, with an accompanying drop in temperature.

May, June and July are characterised by fairly heavy rain, but about the end of July there is a dry spell of some two weeks. Temperatures continue to drop, July and August being the coldest months of the year, with mean monthly temperatures around 77°F. (25°C.).

August and September are months of heavy rain; humidity is high and temperature low. In October, the thunderstorms return, the rains ending somewhat abruptly towards the end of the month. Temperatures, more especially the maximum, begin to rise in September and October.

Over the whole year, the range of temperature is small. In the savannah, where the greatest fluctuations occur, the mean monthly temperature ranges only from 75·3 to 83·7°F. (24·1 to 28·7°C.), with mean monthly maxima varying from 82·2 to 92·2°F. (27·9 to 33·4°C.) and minima from 70·6 to 75·2°F. (21·4 to 24·0°C.). The average yearly rainfall for the first two years was 71·6 in., distributed as shown in Table I; it should be noted that 1956 was atypical, only 50 inches being recorded.

TABLE I.

Monthly rainfall (in.) for the years 1954–1956 at Ugbobigha.

Month	11	12	1	2	3	4	5	6	7	8	9	10	Total
1954 ..	0·7	0·5	0·0	1·7	8·2	7·6	8·9	5·2	5·6	12·0	14·5	7·8	72·7
1955 ..	0·0	0·0	0·0	0·0	5·6	5·3	7·6	6·0	11·7	10·1	12·7	11·4	70·6
1956 ..	0·5	3·0	0·0	1·2	8·2	1·5	9·1	4·4	6·1	1·0	6·0	9·0	50·0

Description of the investigation.

Across the savannah plain a track, 10 to 12 ft. wide, runs northwards from Ugbobigha to Afuje (see fig. 1). This track passes by a small but dense forest island, known as Nash Kurmi, which is some 500 yd. in circumference: just off the track there are three pools frequented by game.

From the beginning of the belt inhabited by *G. longipalpis* to the forest island is 3,200 yd. To start with, this length was divided, according to the character of the vegetation, into six sections (Red, White, Orange, Blue, Yellow and Green), and subdivided into 100-yd. subsections, which were patrolled regularly.

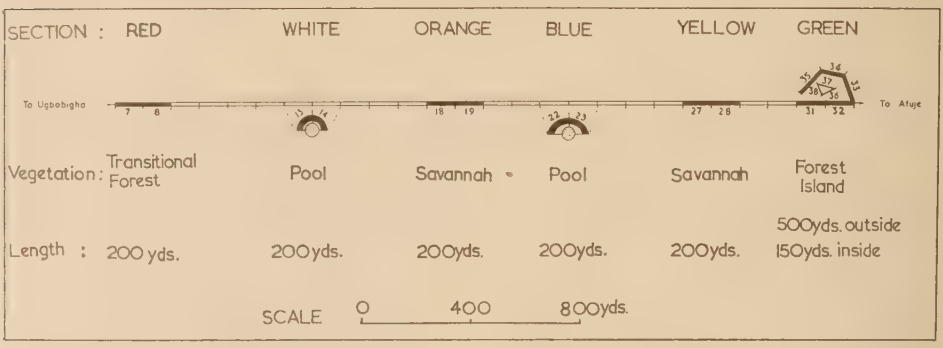


Fig. 2.—Diagram of the fly-round on which the ecology of *G. longipalpis* was investigated.

However, it was soon found that, owing to the limited period of daily activity of the flies, the distance was too great; consequently only certain representative subsections were sampled. The fly-round in its final form is shown diagrammatically in fig. 2, and details are given in Table II.

The team consisted of two catchers and two men who marked and recorded the captures. The actual number of flies captured was divided by two (there being two catchers) and the results were expressed as flies per boy per 100 yd.

TABLE II.

Details of fly-round sections.

Sections	Subsection numbers	Length (yd.)	Description
Red	7, 8	200	Transition forest, bordering a forest island
White	13, 14	200	Along the edge of Pool No. 2
Orange	18, 19	200	Savannah woodland
Blue	22, 23	200	Along the edge of Pool No. 3
Yellow	27, 28	200	Savannah woodland
Green	31–35	500	Outside edge of forest island
	36–38	150	Inside forest island (subsections of only 50 yd. each)

The bulk of the flies was caught on the vegetation, since *G. longipalpis* does not feed readily on man. The fly-round was carried out on two consecutive days at weekly intervals.

The majority of flies caught on these rounds were males. During the last year of the investigation, in order to catch more females, an additional, bait-ox, fly-round was undertaken once a week over the same fly-round path.

Before release, all flies were marked with colours signifying the section where caught and date of capture; recaptures were recorded and released. All flies caught on the ox were given a differentiating mark.

In August 1955, the fly-rounds had to be suspended for six weeks, owing to the presence of a wounded elephant.

The Seasonal Factor.

Introduction.

Two meteorological stations were set up, one in the savannah and one inside the forest island. Each station had a Stevenson screen, containing a wet- and dry-bulb thermometer and a recording thermohygrograph, a Livingston white-bulb atmometer, and a rain gauge. All temperature and humidity readings were taken at 4 ft. above ground level.

The savannah station was set up to give a general picture of the climate of the area. The forest-island station was in a glade, where trees with a canopy about 20 ft. high made sufficient shade to suppress the undergrowth.

Comparison between the climate in the savannah and in the forest island.

Starting in November, at the beginning of the dry season, the average monthly figures over the three years for the various climatic factors are shown graphically in fig. 3.

(*i*) *Evaporation rate.*—During the dry season the evaporation rate in the savannah is much the higher, averaging in January, for example, 31·3 cc. as against only 15·1 cc. in the forest island. The difference then decreases, becoming slight in the heavy rains. It should be noted that the evaporation rate for August is normally only 3–4 cc., but the average figure over the three years has been greatly increased by the failure of the rains in August 1956, when the evaporation rate was 11 cc.

(*ii*) *Saturation deficit.*—At all times of the year, the forest island is more humid than the savannah; the difference in saturation deficit is greatest in February, when in the savannah it is 1·3 mb. higher, but least in July, when the difference is only 0·2 mb.

(*iii*) *Temperature.*—The temperature of the forest island is more equable than that of the savannah. Minimum temperatures are very similar, but in January the forest island is 2°F. warmer; however, the maximum temperatures of the forest island are appreciably lower, especially in December, when the difference is as great as 7·4°F. But after the reduction in vegetational insulation caused by defoliation and the January grass fires the temperature difference drops to only 3·5°F. in February, the month when the highest maximum temperatures are recorded.

Clearly the forest island has an ecoclimate that is both cooler and more humid than that of the surrounding savannah, thus providing the fly with milder conditions, when required.

Climatic variations in the three years.

Of the three years of the investigation, 1954 and 1955 were very similar, but in 1956 the rainfall was only 50·0 in. as against the average of the previous two

years of 71·6 in. The main differences were a dry April (1·5 in. as against 6·5 in. average), a dry August (1·0 in. as against 11·0 in. average), and a dry September (6·0 in. as against 13·6 in.). During December, on the other hand, which is usually dry, 3·0 in. of rain were recorded. The result of these abnormalities in the rainfall of 1956 was that the evaporation and saturation deficit were exceptionally high throughout the wet season, but unusually low in December. No appreciable temperature differences were detected.

Fly-round results when man was used as the bait.

G. longipalpis has a pronounced rhythm of diurnal activity, being inactive below a certain temperature, found by Morris (1934), and by work at Ugbobigha,

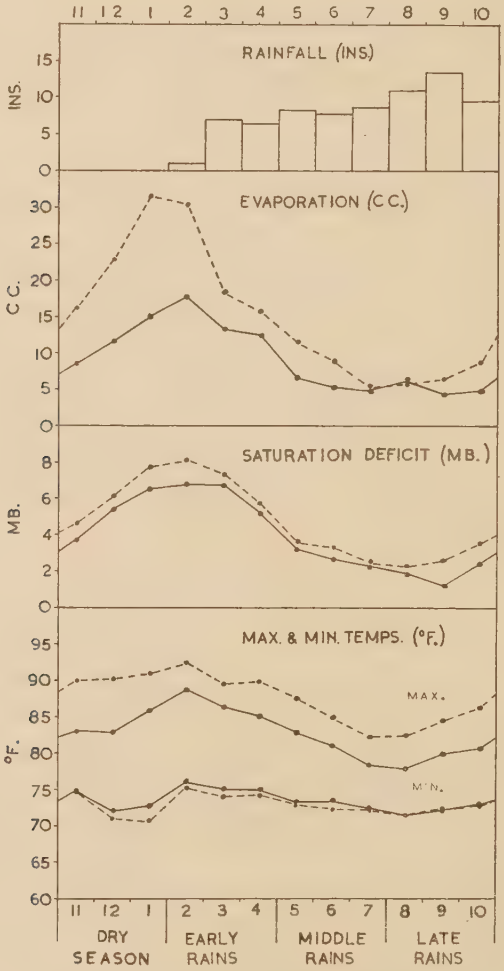


Fig. 3.—The difference in climate between the savannah (broken line) and forest island (continuous line). Data used is the average for three years, 1954–1956, except rainfall, which is the average for two years, 1954–1955.

to be about 74°F. (23°C.). Fly-rounds were therefore not started until this temperature was reached. Since the fly-rounds were patrolled in opposite directions on alternate days (that is, from subsection 7 to subsection 38 on one day, and from 38 to 7 on the next day), errors that may have occurred owing to fluctuations in the activity rhythm of the flies should have been reduced to a minimum.

It should be remembered that the sample of flies caught may not represent the same proportion of the total population at all seasons of the year; Morris (1934), working on *G. longipalpis* in Ghana, called his fly catches a measure of "density-activity". As regards the work at Ugbobigha, it is thought that the fly-round catches did reflect the size of the population, particularly as similar fluctuations in size of catch were obtained on both man and ox fly-rounds.

(*a*) *Seasonal fluctuations in male fly density.*—Owing to the scarcity of females appearing to man, results are given for males only. The monthly total of male flies caught on the fly-round is shown graphically in fig. 4; it will be seen that fly density fluctuates considerably during the year.

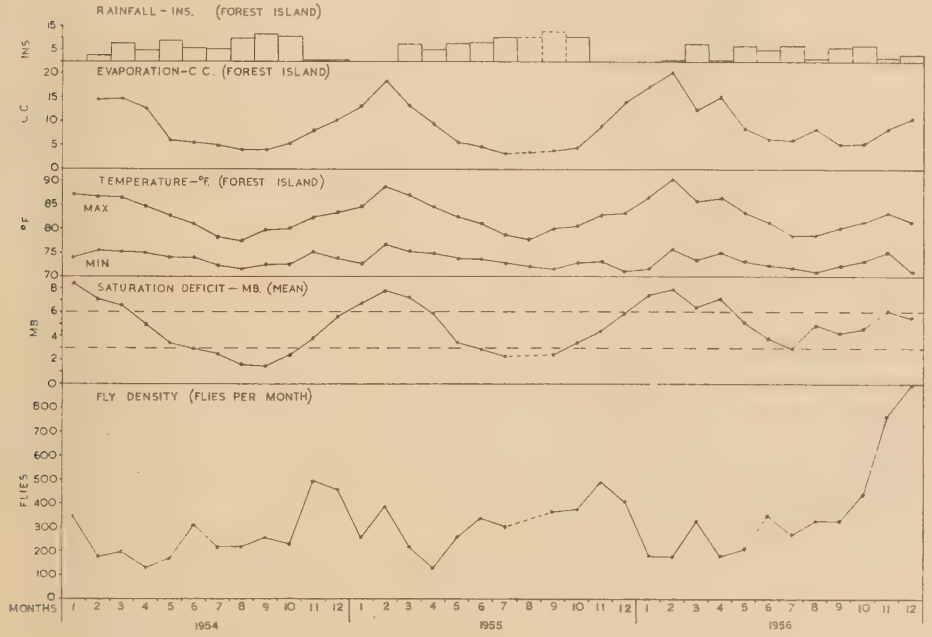


Fig. 4.—The seasonal fluctuations in fly density of males of *G. longipalpis* on the man fly-round, together with relevant meteorological data.

The lowest catches are made in April, when the evaporation rate and temperature are falling from their dry-season maxima, and when conditions are just starting to become more favourable for the fly. The catches then start increasing with the improving climatic conditions, until a minor peak is reached in June, in the first part of the rains. Conditions would then appear to become too wet as there is a definite drop in the size of the catch which remains at a median level before rising to the highest peak of the year in November, when the rains

have ceased. Thereafter the catches tend to fall irregularly as the dry season conditions become more severe, until once more they are lowest in April.

Since flies are able to utilise any type of vegetation and climate varying between the extremes found in the forest island and the savannah woodland, respectively, it seems reasonable to use the mean of the monthly figures from these two extremes when studying the seasonal relationship between the fly population and the climate.

It appears from fig. 4 that there is a relationship between the fly density and the mean monthly saturation deficit. When the saturation deficit is high, the catches fall; when the saturation deficit is low, the catches also fall, but when the saturation deficit is intermediate, the population thrives.

TABLE III.

To show the relationship between fly density and saturation deficit.

Saturation deficit (mb.)	No. of months	Av. fly density (flies per boy per 100 yd.)	
		Same month	One month later
8–9	—	—	—
7–8	6	5·2	5·4
6–7	4	10·6	10·6
5–6	6	10·5	7·0
4–5	4	11·3	13·5
3–4	7	9·6	10·4
2–3	5	8·0	9·1
1–2	2	6·2	6·4
0–1	—	—	—

Such a relationship is likewise clearly indicated in Table III, which shows the number of months in which the saturation deficit fell into a given 1-mb. group (column 2), followed by the average fly density for those months, and for the month after. The figures suggest a distinct relationship between the fly density and the saturation deficit of the same month; further, that the saturation deficit can be too high as well as too low, optimal conditions being associated with saturation deficits of 4–5 mb. Saturation deficits below 2 or above 7 mb. appear relatively adverse.

TABLE IV.

To show the relationship between mean monthly temperature and fly density.

Temperature (°F.)	No. of months	Av. fly density (flies per boy per 100 yd.)	
		Same month	One month later
81–83	2	6·3	6·5
79–81	11	7·4	7·7
77–79	8	9·6	12·7
75–77	9	11·0	9·3
73–75	4	7·7	8·8

From Table IV it would appear that there is also a relationship between mean monthly temperature and the fly density of the same and the following month; further, that a temperature of about 77°F. (25°C.) is optimal. It is known that temperature exerts a strong influence on the rate of reproduction in other species of tsetse.

From these figures, the most favourable conditions for the fly in the field appear to be associated with a temperature of 77°F. (25°C.) and a saturation deficit of 4–5 mb., which would be given at that temperature by a relative humidity of 85 per cent. Such climatic conditions should therefore be suitable for the maintenance of *G. longipalpis* in the laboratory.

(*b*) *Seasonal distribution of* G. longipalpis *in relation to the vegetation.*—As has been stated, the fly-round tapped five different types of vegetation—the inside and outside of the forest island, the pools, transition forest and savannah woodland.



Fig. 5.—Monthly fluctuations in percentage distribution of flies in each vegetation type between August 1954 and July 1955. O.F., outside of forest island; I.F., inside forest island.

Seasonal fluctuations in distribution are shown in fig. 5, which gives the percentage of the total catch caught in each vegetational type during each month between August 1954 and July 1955 (this period has been chosen as typical of the three years). In August and September 1954, the percentage of flies caught inside the forest island was small, the bulk of the flies being caught on the outside and in the more open types of vegetation. With the end of the rains in October, there was a slight decrease in the percentage from the savannah and pools, associated with a slight increase in the inside of the forest island; this trend towards concentration continued throughout the dry season, a progressively larger percentage of flies being caught inside the forest island, and a correspondingly smaller percentage elsewhere. By February 1955, 89 per cent. of the total flies caught were taken in and around the forest island, 63 per cent. being inside; the savannah was virtually evacuated. In April, when the saturation deficit had started to fall, flies were caught equally inside and outside the forest island, and were also caught in the savannah. This movement out from the forest island continued until, by July, only 7 per cent. of the flies were taken inside the forest.

Whereas dispersal undoubtedly takes place, a fall in the forest-island population being associated with an increase in the population of the open country, it cannot be definitely proved that the forest island acts as a concentration site, and not merely as a survival site. Efforts to prove, by marking, that individual flies did concentrate in the forest island failed, as might be expected when one considers the many directions in which flies marked in the savannah might go. On the other hand, some data which suggests that concentration may really take place is given below, the figures being the total number of flies caught in and around the forest island in the relevant months of the last two years:—

	1955	1956
January	204	145
February	343	164
March	178	291
April	107	163

At a time when the fly population was minimal throughout the rest of the fly-belt, there was a marked increase in the forest population in February 1955, and in March 1956.

It is interesting to study this seasonal movement in relation to the saturation deficit. It has been postulated that saturation deficits above 7 and below 2 mb. are adverse, and if this is true, then seasonal dispersal and concentration might be expected to occur just before these limits were reached.

The evacuation of the savannah was complete in the month of December in both 1954 and 1955, when the savannah saturation deficit was 6·2 and 6·1 mb., respectively. Dispersal into the savannah took place in April in 1954 and 1955, and May in 1956, when the saturation deficit was 5·2, 6·3 and 6·2 mb., having fallen from 7·3, 7·2 and 7·9 mb., respectively. It would appear, therefore, that the saturation deficits ranging between 6 and 7 mb. are crucial, in that when such conditions prevail, fly concentration or dispersal will take place, depending upon whether the trend of saturation deficit is upwards or downwards.

There would also appear to be a crucial point at the lower limit, since when the saturation deficit inside the forest is dropping from 3 to 2 mb., the fly population evacuates the centre of the forest in favour of the edge.

The effect of saturation deficit (in mb.) on *G. longipalpis* may be summarised as follows:— above 7—markedly adverse, 6–7—crucial, 5–6—very favourable, 4–5—optimal, 3–4—very favourable, 2–3—crucial, below 2—adverse.

(*c*) *The effect of a prolongation of favourable saturation deficits on the fly population.*—It may have been noticed in fig. 4 that the fly population in 1956 rose to twice the height of the population in 1954 and 1955. Lines have been drawn at the 3 mb. and 6 mb. levels on the saturation-deficit graph in fig. 4 to show the period when the saturation deficit lies in the favourable zone. In 1954 and 1955, this period is short (4–5 months), whereas in 1956, this period is long (8 months). This indicates that a prolongation of the period of favourable saturation deficit leads to an enormous increase in population.

A consideration of the daily evaporation rate (mean of the forest island and the savannah) suggests that values of 6–16 cc. are favourable for the fly, with an optimum zone of 10–14 cc. This contrasts with the optimum zone of 20–25 cc. found for *G. morsitans* Westw. (Nash, 1937); this difference is only to be expected, because the distribution of *G. longipalpis* in Nigeria does not extend nearly so far towards the arid north as does that of *G. morsitans*, but does extend considerably farther into the humid south.

There is some evidence that in years when there is a prolongation of the period in which saturation deficits are favourable, *G. longipalpis* may extend its range. Concurrent with this investigation, fly-rounds were also being undertaken on *G. palpalis* in an area at the southern edge of the *longipalpis* belt. A few specimens of *G. longipalpis* were caught on the *palpalis* round; the average catch in 1954 and 1955 was 69 flies, but in 1956 this total was double, at 137 flies. Of these 137 flies, 53 came from the section of the *palpalis* round which is farthest from the *longipalpis* country, and which had provided in the two previous years an average of only five flies; hence the population of *G. longipalpis* had increased over ten times in this outlying area.

(*d*) *Travel by individual flies in relation to season.*—It was hoped that, by marking flies, more insight would be gained into population movements. However, the results were disappointing, as out of a total of over 18,000 flies marked during the three years, only 294 (1·6%) were recaptured. The number of marked flies known to have travelled over 1,000 yd. is expressed in Table V as a percentage of the total recaptures.

TABLE V.

Extent of travel by flies at different seasons.

Month of marking	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Percentage of recaptures that had travelled over 1,000 yd.	0	0	30	43	13	30	23	21	19	26	16	8

The figures are too small to be valid, but they tend to confirm that there is little travel in January and February, when concentration is complete, much travel in March and April, when dispersal is taking place, a fair amount of travel throughout the wet season, and considerable travel by flies marked in October, which have been recaptured after concentration.

The maximum distance recorded for travel by a fly was 3½ miles. One fly was recaptured on the day of marking having travelled 2,200 yd.

(*e*) *Seasonal fluctuation in sex ratio.*—The number of females caught on the man fly-round was very small; over three years, females amounted to 1·9 per

cent. of the total catch of 10,434 flies. The monthly percentages of females are shown in Table VI.

It can be seen that the highest percentages occur in April and May, when, as will be described later, male flies exhibit the greatest hunger.

TABLE VI.

The percentage of females in the total monthly catch on the man fly-round (3 years).

Month	Total females	Percentage females
January	8	1·3
February	21	3·2
March	30	4·5
April	31	7·7
May	51	8·6
June	17	2·0
July	16	2·3
August	5	1·1
September	7	0·7
October	2	0·2
November	5	0·3
December	3	0·2

Results of fly-rounds using a bait-ox.

The ox fly-round differed from the man fly-round in that it was carried out only once a week and was patrolled in the same direction every time, *i.e.*, from 7 to 38. Hence whenever comparisons are made for these two types of round.

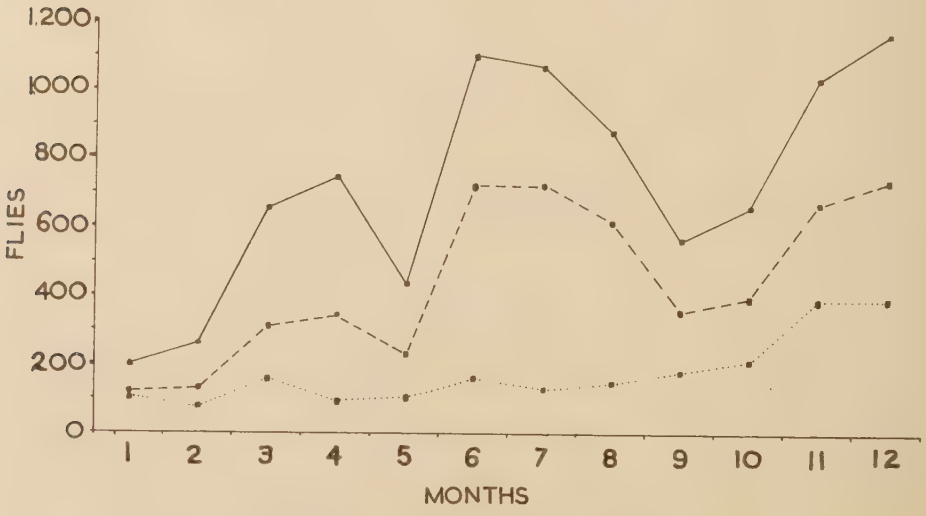


Fig. 6.—The seasonal fluctuations in fly density of *G. longipalpis* during 1956 as shown by catches on the ox fly-round and man fly-round. ———, ox fly-round, both sexes; – – –, ox fly-round, males only; ....., man fly-round, males only.

data from the man fly-round are only given for the outward journey, *i.e.*, 7 to 38, and not for 38 to 7.

(*a*) *Seasonal fluctuations in fly density.*—The seasonal fluctuations in fly density are shown on fig. 6; the figures used are the total catch per month. The upper curve gives the picture for both sexes when caught off an ox; the lower two curves are for males only, and show the difference between the catches obtained when ox or man forms the bait.

It is clear from the curves for the ox fly-round that the inclusion of females in the catch does not affect the picture, even though they form nearly 40 per cent. of the catch. Further, far greater number of flies are caught when an ox is used.

Considering the catches of males only on the ox fly-round (broken line) and man fly-round (dotted line) it will be seen that there are two periods when the fluctuations are dissimilar. In April, the ox fly-round catch shows an increase over the March catch, with a subsequent decrease in May, whereas the man fly-round catch shows a decrease in April, followed by a slight increase. In June, the ox fly-round catch shows a marked increase, and a subsequent decrease from July to September; the man fly-round shows a smaller rise in June, and a slight increase in catch from July to September. These dissimilarities are believed to be associated with dispersal of the fly and difference within the various vegetational types of the size of catches on the ox fly-round relative to catches on the man fly-round; these are discussed further in a later section (see pp. 611–612).

(*b*) *Seasonal distribution of* G. longipalpis *in relation to the vegetation.*—Seasonal variations in catches in the various vegetation types are not so pronounced on the ox fly-round, but the importance of the forest island as a survival site is again manifest. Using males only, to facilitate comparison with the man fly-round, 81 per cent. of the flies caught in February 1956 on the ox fly-round came from the forest island, and only 2 per cent. from the savannah; comparable figures for the man fly-round (which was done concurrently) were 96 and 0 per cent., respectively. The ox fly-round also demonstrated wet-season dispersal from the inside of the forest island.

Figures for the ox fly-round suggest that females are less inclined than males to evacuate the forest island in the rains.

(*c*) *Seasonal fluctuations in sex ratio on the ox fly-round.*—Of the 8,757 flies caught on the ox fly-round, 39 per cent. were female. The monthly percentages are shown in Table VII.

The percentage of females is highest from February to May, with a peak in April; this agrees with the findings for the man fly-round.

TABLE VII.

The percentage of females caught on the ox fly-round.

Month	♀♀ (no.)	♀♀ (%)	Month	♀♀ (no.)	♀♀ (%)
Jan.	71	39·6	July	346	32·3
Feb.	128	49·2	Aug.	261	29·7
Mar.	340	51·8	Sept.	205	36·7
Apr.	403	53·8	Oct.	262	39·7
May	201	46·2	Nov.	366	35·4
June	379	34·4	Dec.	424	36·6

Fly breeding.

(*a*) *Results from searching for pupae.*—Owing to lack of time and staff, it was impossible to attempt a detailed study of the breeding sites of *G. longipalpis*, but the figures given below may be of interest, as so little has been published on the subject.

From May 1955 to April 1956, 10 selected log breeding sites at the forest island were examined weekly. Since the number of pupae found was small, the results are grouped by seasons:—

Dry season	(November to January)	45 pupae
Early rains	(February to April)	13 ,,
Rains	(May to October)	0 ,,

These results are typical of those recorded for other species of tsetse, in that they suggest that pupae can readily be found in the dry season but not in the heavy rains when the soil is sticky. Morris (1934), on the authority of Pomeroy, states that no breeding takes place in the dry season, December to March; the results given above certainly do not confirm this statement. Pupae were also found under a white-painted instrument cupboard whose floor was 18 in. above ground level. Two small, open-sided, grass shelters were built within the forest island, but even though the soil remained dry during the rains, no pupae could be found in them.

It is interesting to record that pupae of *G. palpalis*, *G. fusca* and *G. medicorum* were found under the same logs as those used by *G. longipalpis*; this is believed to be the first record of a breeding site of *G. medicorum*.

(*b*) *Breeding of* G. longipalpis *in the laboratory.*—Attempts were made to breed *G. longipalpis* in a mud-walled, thatch-roofed fly-room, in which no climatic control was possible apart from wetting the sacking cupboards. The investigation failed because no method could be found for making this species mate in captivity. Wild-caught females did produce pupae at the rate of 1·2 to 1·6 pupae per female per month.

The Food Factor.

During the three years, the hunger stage of all flies caught was recorded, using the simple method described by Nash (1937). Any spoor and any animals seen on the fly-round were also recorded.

The hunger staging of flies taken on the bait-ox is inaccurate, because some of the flies will have started to feed before being caught. The results from the man fly-round (non-teneral males only) are shown in Table VIII.

It will be noted that hunger is consistently greater from February to May inclusive. The grass is deliberately burnt in game drives in January or February; this period corresponds with the season when there is least cover and when man is most active in hunting. It is therefore possible that the fly is constantly losing touch with its host.

Hunger is least at the start of the dry season, November and December, when the unburnt elephant grass is 10–15 ft. high and almost impenetrable to all but the largest animals, and so probably restricts widespread movement of game. It seems likely that by this season the fly has established intimate contact in restricted areas with its hosts, the game being as yet unharried by man. Owing to the cover of elephant grass throughout the area, records of game seen whilst the fly-round is being undertaken suggests that game is exceedingly scarce; that this is a completely false picture is shown by the game drives, when a considerable number of animals may be killed.

The following animals (excluding small or rare ones) are known to be present in the area, mainly from examination of hunters' kills: Maxwell's duiker, *Cephalophus maxwellii*; red-flanked duiker, *Cephalophus rufilatus*; crowned duiker, *Sylvicapra grimmia*; bushbuck, *Tragelaphus scriptus*; red river hog, *Potamochoerus porcus*; dwarf forest buffalo, *Syncerus nanus*; African savannah elephant,

TABLE VIII.

The percentage of non-teneral males that are hungry (3 years' data combined).

Month	Total non-teneral males	Hungry non-teneral males	Percentage hungry
January	590	19	3·2
February	625	31	5·0
March	624	38	6·1
April	356	31	8·7
May	534	40	7·5
June	1126	30	2·7
July	640	14	2·2
August	502	24	4·8
September	853	19	2·2
October	1031	20	1·9
November	1738	24	1·4
December	1749	21	1·2

Loxodonta africana; waterbuck, *Kobus defassa unctuosus*; mona monkey, *Cercopithecus mona*; patas monkey, *Erythrocebus patas*; tantalus guenon monkey, *Cercopithecus aethiops tantalus*.

The commonest animals are duiker and bushbuck. Pig is also fairly common and elephant visits the area from June to October or November.

The greatest insight into the food preferences of *G. longipalpis* is being given by the precipitin tests carried out by Mr. B. Weitz of the Lister Institute (Weitz, 1956). He has tested smears of blood-meals sent to him against sera of the commoner and more likely hosts. Some of the smears were of poor quality and so could only be assigned to the family Bovidae. No serum was available from the red river hog, but "unidentified Suid" feeds must be from this species, as it is the only Suid occurring in the area, and sera of wart-hog, bushpig and domestic pig all gave negative results.

The positive results are given below:—

Host	No. of feeds	%
Bushbuck	23	53
Buffalo	4	9
Unidentified Bovid ..	9	20
Red river hog	8	18
Total	44	100

These show that *G. longipalpis* feeds to a great extent on bushbuck and not on the smaller antelopes, although these occur in great numbers. Morris (1934) concluded from various lines of evidence that *G. longipalpis* could maintain itself entirely on bushbuck and duiker; the above evidence confirms his conclusions as regards bushbuck.

Vegetation.

The distribution of *G. longipalpis* in the different vegetational types at various seasons has already been discussed (p. 603). The vegetation of each type will now be described and analysed with regard to its attractiveness to the fly, as shown by catches on the man and ox fly-rounds, for the whole year. The species composing the vegetation are given in the Appendix (p. 615).

Description of vegetational types.

In the following descriptions, numbers refer to subsections of the fly-round, see figs. 1 and 2.

(*a*) *The forest island.*—The forest island contains a number of tall trees, forming a discontinuous canopy; inside the island there is an area (36) of low thicket, a tangle of shrubs, climbers and young trees presenting an impenetrable mass of vegetation 12 ft. high; a second area (38) consisting of small trees roofed over at about 12 ft. with a tangle that is so dense that all the undergrowth is suppressed; and a third area (37) comprising an open glade, where the closed canopy of the middle storey suppresses the undergrowth, surrounded by shrubs which are sufficiently sparse on the west side for the savannah to be visible. Externally, the edge of the forest island is sharply defined. The undergrowth forms an impenetrable barrier on the side nearest the road, but is less dense on the savannah side.

(*b*) *Pools vegetation.*—The formation of the vegetation around the two pools is similar. Towards the south (13 and 22) the fringe of vegetation is narrow, consisting of a row of tall widespreading trees (*Brachystegia curycoma*, *Erythrophleum guineense*) with little undergrowth; towards the north (14 and 23) the fringe of vegetation is wider, the tall trees being scattered, with shrubs beneath them. Pool 2 (13–14) is 30 yd. in diameter, and Pool 3 (22, 23) about 80 yd.

(*c*) *Transition forest.*—The vegetation here is typical transition forest, consisting of trees forming a more or less continuous canopy with shorter savannah grasses and forest shrubs beneath. Its western edge borders a forest island, which approaches nearer to the road in 8, resulting in the vegetation being thicker there than in 7.

(*d*) *Savannah.*—The savannah vegetation is typical of the region, consisting of small trees and coarse elephant grass 10–15 ft. high.

TABLE IX.

The attractiveness to *G. longipalpis* of various vegetational types, when man and ox, respectively, are used as bait.

Round	Sex	Year	Savannah	Transition forest	Pools	Forest island
Man ..	♂	1954	32	46	84	155
„ ..	♂	1955	22	40	78	181
„ ..	♂	1956	34	55	128	267
Man ..	♂	1954–56	88	141	290	603
Ox ..	♂	1956	257	348	347	382
„ ..	♀	1956	163	215	195	274
Ox ..	♂+♀	1956	420	563	542	656

The differences in attractiveness of the various vegetational types on the man and ox fly-rounds.

It has been shown that catches on the ox fly-round are much larger than on the man fly-round. This difference occurs in all vegetational types, but its extent varies greatly according to the nature of the vegetation.

The total flies caught per year per 100 yd. on the man and ox fly-rounds for each vegetational type are shown in Table IX, calculated on a basis of four rounds per month, to make comparison between ox and man fly-rounds simpler.

It will be seen that on both man and ox fly-round the largest catches are made in the forest island, and the smallest in the savannah, but that the savannah catch, relative to the forest, is much larger on the ox fly-round. In the transition forest, the catch of males on the man fly-round is much lower than around the pools, but on the ox fly-round, the catches are similar.

It would appear, therefore, that it is in the more open types of vegetation that the ox attracts relatively far more flies than man; the more detailed analysis made in Table X indicates that this is the case. The total male flies caught in 1956 on the ox fly-round and man fly-round, and the ratio between the two is given in that table.

TABLE X.

The ratio of ox fly-round catches to man fly-round catches in various subsections.

Vegetation type	Sub-section	Catch on ox	Catch on man	Ratio of catches Ox:man	
Savannah ..	—	1030	152	6·8	
Transition forest ..	—	697	102	6·8	
Pools vegetation ..	—	1390	431	3·2	
Forest island ..	—	2246	1480	1·5	
Transition forest ..	7	376	38	10·0	Vegetation thicker in 8
	8	321	64	5·0	
Pools vegetation ..	13	544	126	4·3	No shrubs
	14	307	89	3·4	Shrubs
	22	286	96	3·0	No shrubs
	23	253	120	2·1	Shrubs
Forest island ..	37	222	41	5·4	Glade in forest
	38	114	26	4·4	Open, under low dense canopy
	34	334	132	2·5	Light thicket
	32	292	169	1·7	Thicket
	35	302	176	1·7	Thicket
	33	311	224	1·4	Thicket
	31	332	294	1·1	Dense thicket
	36	339	418	0·8	Very dense low thicket

The upper part of the table deals with the main vegetational types and illustrates plainly that the ox:man ratio is much greater in the first two types of vegetation, which are thicketless, and least in the dense forest island.

The lower part of the table shows that even when the data for the last three vegetational types are broken down into subsections, the principle still holds good that when the vegetation is open, the catches on the ox are proportionally greater.

The flies caught on the ox fly-round were hungrier than those caught on the man fly-round. Even though many flies fed on the ox before being caught, 7·9 per cent. of the 4,950 flies taken on the ox were 'hungry', as against 2·7 per cent. of the 4,387 flies on the man fly-round. This indicates that the ox attracts a larger percentage of the hungry element of the population; hence, if the fly was using only certain types of country for feeding, one would expect to find, in such areas, a higher ratio of catches on the ox fly-round to those on the man fly-round than in areas not so used. Reference to Table X shows that the highest ratios are found in the savannah, and the lowest in the forest island. Thus *G. longipalpis*, like *G. morsitans*, uses open country as feeding grounds.

The use made by G. longipalpis *of the different types of vegetation.*

Even though the main belt of tropical rain-forest bounded the *longipalpis* country on its southern side, this species of tsetse made no use of it. Concurrently with this work, fly-rounds were being undertaken with a bait-ox in the rain-forest, but apart from two specimens caught near the road, *G. longipalpis* was never found.

Islands of forest within the savannah, or the fringing forest of streams that penetrate the savannah, provide the permanent habitats for *G. longipalpis*; in the hot, dry weather the fly can retreat into the densest thickets, or in the heavy rains move out to the edge of the forest.

Pools, out in the savannah, encircled by rather heavier vegetation, serve as temporary habitats which are used by the fly for many months of the year, but become untenable when the water dries up. In the rains they become re-colonised when the flies disperse from the permanent habitats. The pools are seasonally much frequented because they attract game.

When transition forest occurs on the edge of a permanent habitat, it is used as a feeding ground throughout the year, unlike the savannah woodland, which serves this purpose only for so long as the climate permits.

The area where the present investigation was carried out is considered to be typical of *longipalpis* country in Nigeria; it is also typical (T. A. M. Nash, personal communication) of conditions found north of the forest belt in Ghana, referred to by Morris (1934) as "the Inland Savannah Forest round Kintampo, Yeji and Kpeve". However, such conditions are entirely different from those in the coastal plain of Ghana, where Morris carried out his main investigation.

The Trypanosome Infection Rate in *G. longipalpis*.

From April 1954 to March 1957, 4,360 males of *G. longipalpis* were collected from a place about six miles from Ugbobigha and dissected for trypanosomes, with the following results:—

		% of total dissections	% of mature infections
Number dissected	4,360		
Number infected (mature infections only)	939	21·5	—
,, ,, with *Trypanosoma vivax* group	768	17·6	82·0
,, ,, ,, *T. congolense* group	170	3·9	18·1
,, ,, ,, *T. brucei* group	1	0·02	0·1

The monthly figures show mature infection rates ranging from 10·6 to 36·0 per cent., but there is no suggestion of any seasonal variation in the infection rate. There are two other records of infection rates in *G. longipalpis*, one given by Fontoura de Sequeira (1935), who found an overall infection rate of 35·3 per cent. in Portuguese Guinea, and the other by Morris (1934) who obtained infection rates ranging from 24 to 29 per cent. during the early rains at Takoradi, in Ghana. Their figures are higher than ours, but it is believed that they both included

immature infections in their totals. Whereas Morris found that about 80 per cent. of the infections were *congolense* group, at Ugbobigha it was found that 82 per cent. of the infections were *vivax* group. Undoubtedly, *G. longipalpis*, being so readily infected, must be a species of very great economic importance. It is probable that the absence of Zebu cattle from the well-watered grasslands of northern Benin is due to the presence of this tsetse.

It is worth recording that despite the excessively high challenge, the bait-ox was kept free of trypanosomes by the 2-monthly administration of antrycide pro-salt given at a dose rate of 11·7 mg. per kg. body weight. During the 20 months after purchase, the animal's weight increased from approximately 170 to 400 kg.; since no supplementary feed was given, this suggests that there can be nothing wrong with the local grazing and that Zebu cattle might flourish in the grasslands were it not for the presence of tsetse.

Discussion.

The most remarkable and important fact that has emerged from this investigation is that even under the climatic conditions found at Ugbobigha, which is near the southern, humid limit of the range of this species, *G. longipalpis* is so highly sensitive to saturation deficits of over 7 mb. that it is forced to seek sanctuary in forest islands for a few months of the year.

The most northerly place at which we have found this species of tsetse in Nigeria is Guni, between Minna and Kaduna, where the rainfall must be about 53 in. as compared with 70 in. at Ugbobigha. In open country, the average maximum saturation deficit for the hottest, driest month of the year must be about 40 mb. at Guni, as compared with 20 mb. at Ugbobigha.

No detailed investigations have been undertaken on *G. longipalpis* in the Northern Guinea zone, but presumably, under such conditions, this species must be entirely dependent for some six months of the year upon the microclimates found in riverine forest, and therefore could be eradicated very readily by only a small amount of partial clearing, which would permit the entry of hot, dry winds and raise the saturation deficit to as high as 40 mb. At Ugbobigha, a similar method might be effective, but there one would be faced with the extremely rapid rate of regeneration of the vegetation, which would make the maintenance costs prohibitive.

Summary.

A population of *Glossina longipalpis* Wied. was studied in southern Nigeria, in derived savannah of the Southern Guinea zone type, between November 1953 and December 1956. Regular fly-rounds were carried out, using man as bait, and during the third year also using an ox as bait. Meteorological records were taken in the savannah woodland and within a forest island; the latter is cooler and more humid than the former.

The forest-island type of vegetation, with dense thicket under high shade, is the permanent habitat of the fly, although the inside of the forest apparently becomes too humid in the heavy rains, when the flies move out to the edge. Seasonal pools in the savannah, encircled with rather thicker vegetation, form temporary habitats during the rains and early dry season. Transition forest and woodland savannah, when in association with permanent habitats, are used as feeding grounds. During the dry season, the flies concentrate in and around the forest island, and evacuate the woodland savannah, which they recolonise in the early rains.

Fly concentration appears to be associated with saturation deficits (S.D.) reaching 7 mb. or over in the savannah, whereas dispersal is associated with an S.D. dropping to 6 mb. or below. When the mean monthly temperature is

compared with the mean fly densities in that and the succeeding month, the value associated with the greatest density is about 77°F. The optimum saturation deficit, similarly judged, is 4–5 mb.; values below 2 or above 7 mb. appear to be relatively unfavourable. These observations suggest that laboratory cultures of *G. longipalpis* should be kept at 77°F. and 85 per cent. relative humidity.

Fly catches are at a minimum in the early rains (April). They then increase rapidly, level off in the mid-rains, and increase again rapidly to reach their peak in the early dry season (November). The decrease in catches during the dry season represents the adverse effect of high temperature and low humidity on the population, but the continuing decrease during the early rains is believed to represent the effect of fly dispersal, and not a further decrease in population.

In general, catches from the ox fly-round showed the same seasonal fluctuations in fly population as those from the man fly-round, although female flies constituted 39 per cent. of the total catch from the former and only 1·9 per cent. of the total from the latter. The catch is larger from an ox, which attracts more hungry flies (7·9 per cent. of all those caught, against 2·7 per cent. on man). The catches from the ox are higher, in relation to those from man, in the conventional feeding grounds, such as transition forest and woodland savannah, than in the permanent habitat. The proportion of hungry flies amongst non-teneral males caught from man is a maximum in the late dry season and early rains, after the grass fires; good visibility then facilitates hunting activity by man, and the consequent disturbance of the game may cause the fly to lose touch with its hosts. Conversely, flies are least hungry in the early dry season, by which time they have established intimate contact with the game, whose movement, like that of man, is limited by dense elephant grass, 10–15 ft. high.

Precipitin tests on 44 blood-meals, collected over a long period from gorged examples of *G. longipalpis*, suggest that bushbuck (*Tragelaphus scriptus*) provides the bulk of the meals, but that the red river hog (*Potamochoerus porcus*) is also of importance. Of 4,360 males of *G. longipalpis* dissected, 939 (21·5 per cent.) showed mature infections of trypanosomes (768 of *Trypanosoma vivax* group, 170 of *T. congolense* group, and one of *T. brucei* group, comprising 81·8, 18·1 and 0·1 per cent., respectively, of the infections).

Pupae of *G. longipalpis* were found under logs in the forest island, together with pupae of *G. medicorum* Aust., *G. fusca* (Wlk.) and *G. palpalis* (R.-D.). The pupae could be found throughout the dry season and early rains, but not during the heavy rains, when the soil is sticky.

It is suggested that since *G. longipalpis* becomes concentrated in islands and riverine strips of forest when the mean monthly saturation deficit exceeds 7 mb., it might be eradicated by partial clearing of such habitats, except towards the southern, humid limit of its range, where rapid regeneration of the vegetation would make maintenance too costly.

Acknowledgements.

I wish to thank Mr. M. A. Bird, Field Officer, who assisted me during most of this investigation; also Mallam Abdu Maiyanga, Mr. T. Gabesin and the team who carried out the fly-rounds.

I am indebted to Dr. T. A. M. Nash, C.M.G., Director of the West African Institute for Trypanosomiasis Research, for his interest and advice during the work, and for his very great help in revising the manuscript of this paper.

References.

Fontoura de Sequeira, L. A. (1935). Rapport de la Mission Médicale à la Colonie de Guinée en 1932.—86 pp. Lisbon, École Méd. trop.

KEAY, R. W. J. (1949). An outline of Nigerian vegetation.—52 pp. Lagos, Govt. Printer.

MORRIS, K. R. S. (1934). The bionomics and importance of *Glossina longipalpis*, Wied., in the Gold Coast.—*Bull. ent. Res.* **25** pp. 309–335.

NASH, T. A. M. (1937). Climate, the vital factor in the ecology of *Glossina*.—*Bull. ent. Res.* **28** pp. 75–127.

WEITZ, B. (1956). Identification of blood meals of blood-sucking arthropods.—*Bull. World Hlth Org.* **15** pp. 473–490.

APPENDIX.

The Species of Trees found in the various Sections.

Savannah.

The commonest large tree in the savannah is *Terminalia glaucescens*, and the commonest small tree *Entada sudanica*. Other savannah species such as *Sarcocephalus esculentus*, *Crossopteryx febrifuga*, *Vitex doniana*, *Anona senegalensis*, *Lophira alata* are also fairly common. *Daniellia oliveri* is comparatively rare.

Transition forest.

Besides the savannah trees mentioned above, *Sterculia setigera* (?), *Allophylus africanus*, and *Markhamia tomentosa* are all very common. Tall trees such as *Millettia aboensis*, *Lonchocarpus griffonilanus* and *Albizia zygia* also occur.

Pools.

Brachystegia eurycoma is the commonest tall tree, its bright red young leaves making the pools vegetation an outstanding feature of the landscape in the late dry season; *Erythrophleum guineense*, and *Phyllanthus discoideus* are also present. Amongst the smaller trees, *Mitragyna inermis* and *Fagara* sp. are common.

Forest island.

The upper storey of the forest island is composed of *Alstonia congensis*, one example each of *Cleistopholis patens* and *Sterculia oblonga*; *Maesopsis eminii*, *Millettia aboensis* and *Lecaniodiscus cupanioides* are common components of the middle storey.

© Commonwealth Agricultural Bureaux, 1959.

THE ECOLOGY OF *GLOSSINA PALPALIS* (R.-D.) IN SOUTHERN NIGERIA.

By W. A. Page *

Research Entomologist, West African Institute for Trypanosomiasis Research, Kaduna, Nigeria.

Glossina palpalis (R.-D.) has been extensively studied near its hot, dry limit in the savannah zone of northern Nigeria (Nash & Page, 1953), where it is an important carrier of sleeping sickness; it seemed desirable to study the ecology of this species of tsetse in the wetter south, where, curiously enough, sleeping sickness is virtually absent even though animal trypanosomiasis is a great problem. An investigation was accordingly carried out at the West African Institute for Trypanosomiasis Research (W.A.I.T.R.) Field Station, Ugbobigha, from February 1954 to January 1957.

Methods of Investigation.

Situation and description of the area.

The general situation of the W.A.I.T.R. Field Station has been described in a previous paper (Page, 1959). The investigation was made along a permanent stream, the River Ediavukor, which first runs through farmland, and then enters a forest reserve, which is frequently visited by hunters and fishermen.

Description of the fly-round.

After rising in the tropical rain-forest to the south of Ugbobigha village, the stream flows northwards for a mile before emerging into the savannah woodland belt, where its banks are still heavily forested except where cultivated. Three-quarters of a mile after entering the savannah the stream is crossed by an important footpath, from which point a fly-round was marked out along the next 1,900 yd. of the stream. This length was divided into four sections according to the character of the vegetation bordering the banks, and each was subdivided into 100-yd.-long subsections (see fig. 1). The four sections, of which the first two were much the most open, were as follows, arranged here according to vegetational configuration, not geographical location:—

White—Farmland (yams, cacao and fallow).
Yellow—Narrow, light and discontinuous fringing forest.
Green—Wide, dense fringing forest, flooded by stream in rains.
Blue—Wide, heavy fringing forest.

A fifth section of 1,000 yd. was measured westwards along the important footpath that crosses the stream, as it was hoped to discover something of the dispersal of the flies into the savannah; however, so few were caught that catching was stopped after six months.

The fly-round was traversed twice weekly, once in each direction. All tsetse were marked to indicate the section and date of capture. The catching team consisted of four men—two catchers, one marker and one recorder.

Meteorological records.

Meteorological stations were sited in the three following environments:—

(a) The Savannah Station. Results from this station give a general picture of the climate of the area, and are applicable to *G. palpalis* in that,

* Now at Dept. of Zoology, Sub-Dept. of Entomology & Parasitology, University of Edinburgh.

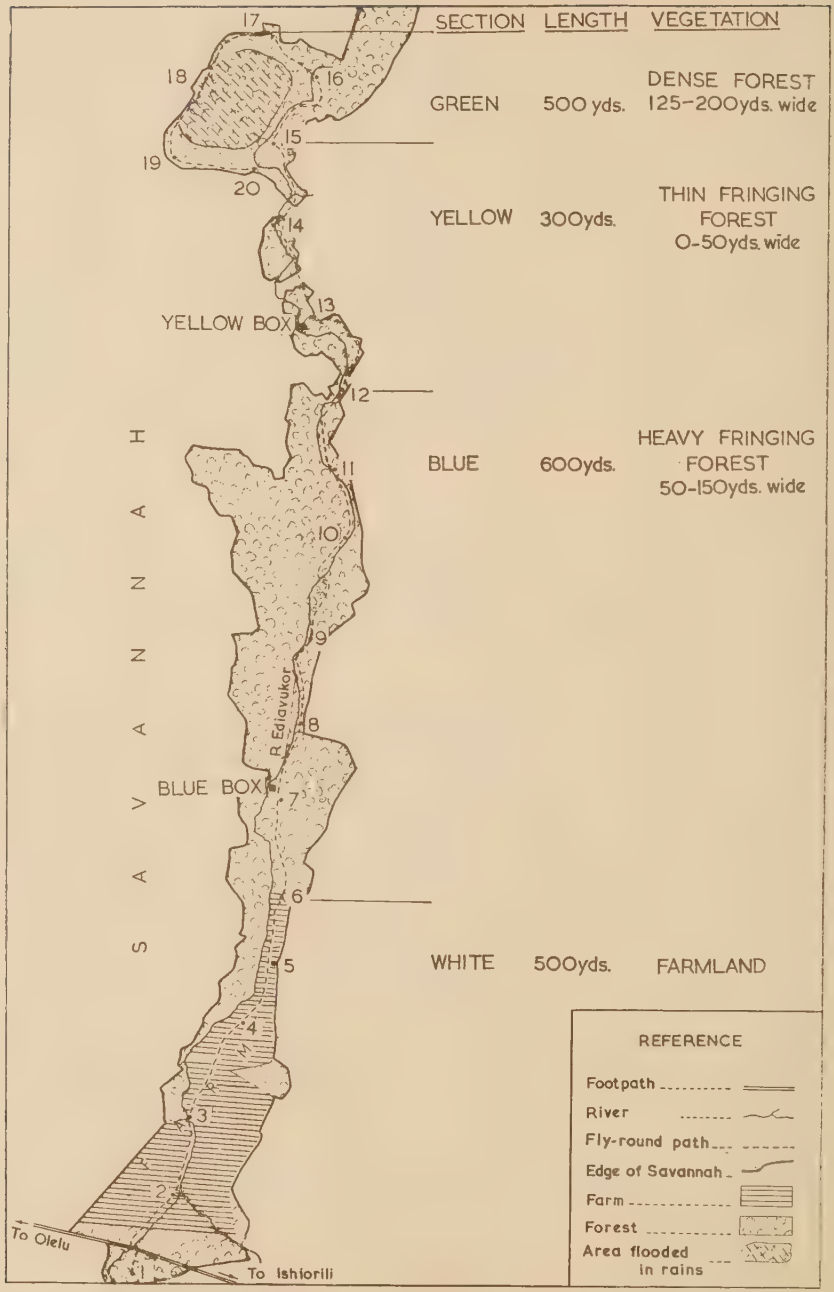


Fig. 1.—The area of the fly-round at Ugbobigha, in southern Nigeria, in which the ecology of *G. palpalis* was investigated. At the points marked "Blue box" and "Yellow box", adults of *G. palpalis*, kept in individual tubes, were housed in boxes for an experiment on length of life (see page 622).

in southern Nigeria, specimens may be caught in farmland and savannah woodland at all times of year.

(b) The Forest Belt Water-hole. This station was just within the high-forest belt, and was sited at the Ugbobigha village water-hole, on the R. Ediavukor, at the bottom of a 20-ft.-deep ravine. The site was south of the fly-round area, but was chosen because *G. palpalis* does occur beside the water-hole and within the high forest; it was thought that records from such a humid, heavily forested area would be of interest for comparison with figures already obtained from a water-hole in a northern Nigerian stream-bed (Nash & Page, 1953).

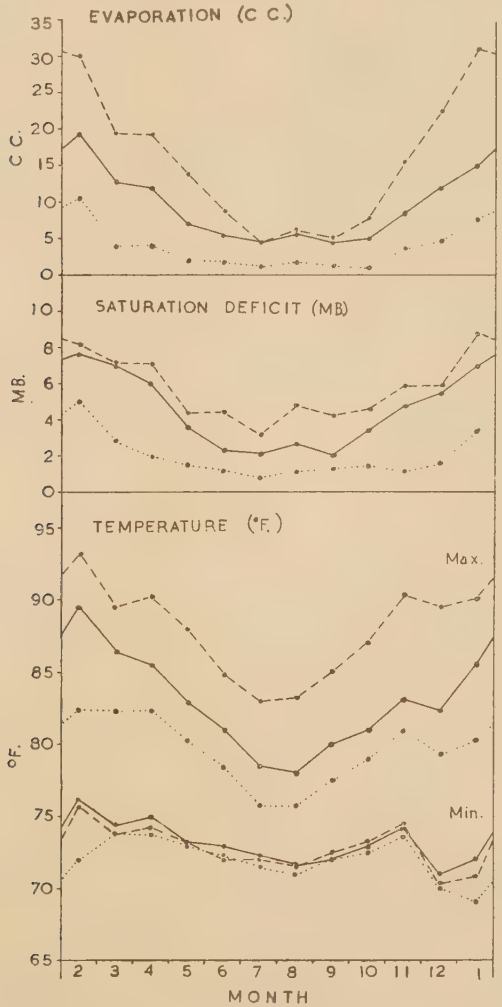


Fig. 2.—The difference in climate between the savannah woodland (broken line), the forest island (unbroken line) and the forest belt water-hole (dotted line). Data used is the average for the years 1955 and 1956.

(c) The Savannah Forest Island Station. This waterless island of forest within the savannah was chosen because it forms a permanent habitat of *G. longipalpis* Wied. (Page, 1959), but it is thought that the records from this island, being intermediate between those of the other two stations, should be employed in this paper, as *G. palpalis* occurs in all three environments.

The meteorological data for the three stations are shown in fig. 2 and indicate the considerable range of climate available for *G. palpalis*. Only the minimum temperature is similar in all three environments.

The climate at Ugbobigha has been previously described (Page, 1959). Briefly, there is a wet season from March or April to October, with a rainfall of about 70 in., followed by a dry season during which the highest maximum and mean temperatures occur.

Results obtained from the Fly-rounds.

Seasonal fluctuations in fly density.

The seasonal fluctuations for the three years of the investigation (fig. 3) show clearly that in this equable climate the population tends to remain steady at a low density, apart from an increase in the second and third months of the rains that is followed by a return to the usual low level during the fourth and fifth months of the rains.

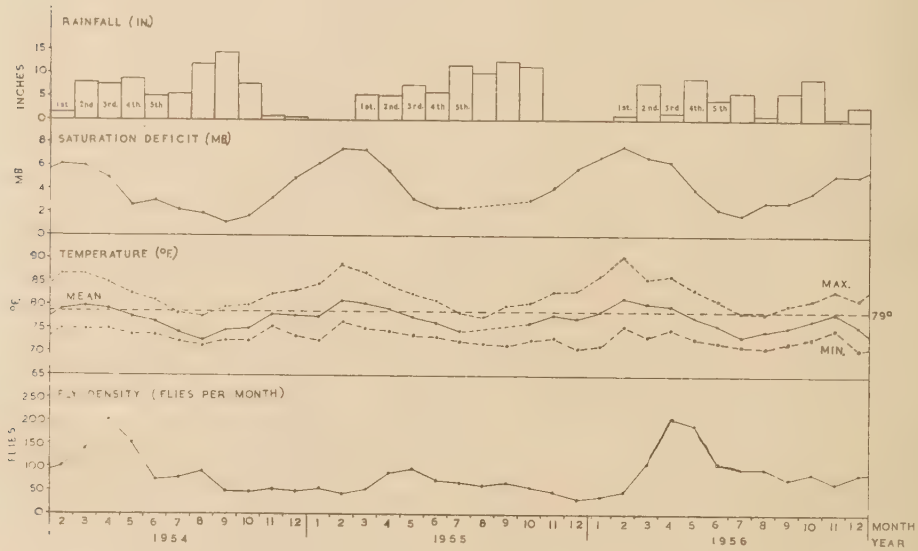


Fig. 3.—The seasonal fluctuations in monthly fly density over three years, together with relevant meteorological data from the station in the forest island.

The rise occurs during the months when the mean temperature is high, lying between 79 and 80°F. (26·1–26·7°C.), and the saturation deficit is falling, the average for the second and third months of the three years being 5·5 mb. Such conditions should stimulate rapid reproduction; Geigy (1948) found that the optimal conditions for the breeding of *G. palpalis* were 79°F. (26·1°C.) and 85 per cent. relative humidity, which give a saturation deficit of 5·0 mb. Nash & Page (1953) suggested from a study of their field data from northern Nigeria that a

temperature of 77°F. (25°C.) with a saturation deficit of 5·3 mb. should be optimal. Subsequently, Nash & others (1959), as a result of work on breeding *G. palpalis* in the laboratory, recommended a temperature of 77–79°F. (25–26·1°C.) with relative humidities ranging from 75 to 85 per cent.; the means of these values give a saturation deficit of 6·5 mb. The climatic conditions during the period of increase thus agrees in general with those suggested as optimal by other workers.

Turning now to the period of decrease, it will be noted that by the fourth and fifth months of the rains the mean temperature has dropped appreciably, which should result in a lower rate of reproduction. If we exclude the saturation deficit figure for May 1956, which was exceptionally high and was associated with only a very slight decrease in population, we find that the average saturation deficit for the fourth and fifth months of the rains in the three years was 2·7 mb. In northern Nigeria, mean monthly saturation deficits below 2 mb. are associated with decreases (Nash & Page, 1953); the present results are not very different.

There can be no doubt that very high humidity is associated with a big reduction in the population of *G. palpalis*. In our investigation in northern Nigeria, where the average annual rainfall was only 47 in. and the climate was much drier, the saturation deficit did not reach the unfavourably low level until August or September, giving a four-month period of population increase, in contrast with only two months at Ugbobigha. The shorter duration of favourable conditions in the south probably explains why the population there never builds up to a really high figure in the wet season.

It will be noted that throughout the latter part of the wet season of 1956, when the saturation deficit was unusually high, the fly population after its April to June decrease remained at an unusually high level for the time of year.

The failure of the population to reach a high level in 1955 may well have been due to the fact that by the third month of the rains the saturation deficit had already become abnormally low at 3·2 mb., as against 4·9 and 6·4 mb. for the third month in 1954 and 1956, respectively; at such a level, which is believed to lie between favourable and unfavourable conditions, one would not expect to get the rapid increase of population that is usually associated with the third month.

Sex ratio.

Of the 3,130 flies caught, 1,424 (45·5%) were female; monthly percentages varied from 65 to 28 per cent., but showed no seasonal trend. The sex ratio does not differ appreciably from that found in the north, where females comprised 49·1 per cent. of 17,306 flies caught (Nash & Page, 1953).

Seasonal distribution of flies within the four sections of the fly-round.

The year can be divided into four seasons, each of three months. Of the total flies, of both sexes and all ages, caught in each season, the percentage occurring in each section (White, Yellow, Green and Blue) is given in Table I for the three years of the investigation.

The basic fly figures were first adjusted to compensate for the differing lengths of the sections; hence, if the flies were distributed uniformly, one would expect 25 per cent. of the catch to occur in each of the four sections. That this is not so, is plain from Table I. There is clearly some environmental effect, most marked in the case of the wide and heavy fringing forest of the Blue section which is almost always the least attractive. Even in the dry season there is no suggestion of the fly seeking the heaviest vegetational types (Green and Blue) as would be the case in northern Nigeria. In the late rains, when the rainfall is greatest, the flies would seem to seek the open farmland of the White section in preference to the other vegetational types.

It seemed possible that the unattractiveness of the heavily forested Blue section

might be due to climatic conditions inimical to fly longevity. A comparison was therefore made between the length of life of flies kept in boxes in this section and in the much more open Yellow section.

Newly emerged adults of *G. palpalis* were put into separate tubes and fed. Next day, after discarding any dead flies, the tubes were numbered, and half taken to one section and half to the other. The flies were kept in well-ventilated boxes, and given an opportunity to feed on a goat each day. The experiment was started on 1st December 1954, and continued until 23rd March 1955, by which time the rains had commenced. A maximum and a minimum thermometer were kept in each box, and read daily.

TABLE I.

The percentage of the total flies, caught in each season, occurring in each section.

Season	1954				1955				1956			
	W	Y	G	B	W	Y	G	B	W	Y	G	B
Early rains Feb.–April	20	35	26	19	32	27	24	17	20	36	25	19
Middle rains May–July	35	25	26	13	29	33	22	16	26	29	28	17
Late rains Aug.–Oct.	40	21	19	19	29	26	21	24	36	28	20	17
Dry season Nov.–Jan.	33	33	17	17	21	25	36	18	27	34	23	16

The results are shown in Table II. There was no appreciable difference in the length of life of flies kept in the Yellow and Blue sections, nor were there any temperature differences except that the minimum temperature was some 3°F. (1·7°C.) lower in the Blue section.

TABLE II.

The average length of life of adults of *G. palpalis* kept in tubes in the Yellow and Blue sections of the fly-round.

Month	No. of flies put in each box	Average length of life		Average temperature (°F.)			
				Maximum		Minimum	
		Y	B	Y	B	Y	B
December	50	50	55	82	82	69	65
January	41	23	27	84	84	68	65
February	31	22	22	87	88	73	70

Clearly, the environment of the Blue section is not inimical to the fly, provided that there is an assured supply of food.

The low period of survival shown by the experimental flies in both sections in January and February is believed to be due to the high maximum temperatures from which the flies could not escape.

The vegetational preferences of G. palpalis.

No major seasonal movements of the fly population from one section to another could be detected. Since, however, it seemed possible that there might be localised preferences, the data for each 100-yd.-long subsection have been examined.

The number of flies caught over a period of three years in each subsection during each season of the year is shown in Table III. If the total catch of 3,194 flies be divided by 19 (the total number of subsections) the average per subsection is 168; deviations from this figure should indicate the degree of localised preference by the fly. The table should be examined in conjunction with the map (fig. 1).

It will be seen that in almost all the White subsections, where the land is farmed and visibility is therefore good, the catches are above average; the particularly high catch on subsection 1 is attributable to the much-used inter-village track, which crosses the fly-round. In contrast, in the Blue section, which passes through heavy forest with thick undergrowth and greatly restricted visibility, the catches are below average in all the subsections but one (number 11), where the forest is thinning out. The catches for the Yellow section, which runs along the edge of very narrow, discontinuous, thin, fringing forest, are well above average in all subsections. These results suggest that open farmland and the edge of narrow forest, in both of which visibility is good, are attractive, but that the inside of dense forest is unattractive.

The picture for the Green section is not quite so straightforward. The catch for subsection 15 is rather below average, which might be expected, because it is well within dense forest; that on 16 is rather higher, and the forest at this point is so thin that one can see out into the savannah. Catches on 17 and 18 are well below average; these skirt the forest edge, which is here very swampy, so that the adjacent savannah grass grows to a height of 15 feet and remains too wet to burn properly; visibility is consequently very poor. Subsection 19 also skirts the forest, but is much drier, and the savannah grass does not exceed a height of 5–6 ft.; here the catch is well above average. Thus, results from the Green subsections in no way contradict the conclusions reached in the previous paragraph.

Presumably the preference shown by the fly for sites with good visibility is associated with searching for food; this must be a very important factor with *G. palpalis* in southern Nigeria, where the luxuriant vegetation provides ample cover for game.

It is worth recording that cacao plantations are attractive to fly in the middle and heavy rains, but less so in the dry season and early rains.

The savannah woodland was not tapped by the fly-round, but fortunately data are available from specimens taken on the *G. longipalpis* fly-round (Page, 1959), which tapped 400 yd. of savannah woodland at a distance of $\frac{1}{2}$–$1\frac{1}{2}$ miles from the nearest stream. During three years, 34 examples of *G. palpalis* were taken, the seasonal distribution being as follows:— early rains, 11; middle rains, 17; late rains, 4; dry season, 2. As on the main fly-round, *G. palpalis* was most numerous in the early and middle rains. Odd specimens of *G. palpalis* were frequently found in the camp, which was situated in savannah woodland, $\frac{1}{2}$ mile from the nearest stream. This is a very different picture to that found in northern Nigeria, where this species is entirely riverine in habit, specimens being very rarely encountered in the savannah, and then only during the period of heaviest rainfall.

To the south of the camp and the fly-round lies the main and continuous belt of tropical rain-forest. *G. palpalis* does occur in very small numbers within this forest, and in village clearings lying within this belt.

Fly hunger in relation to season.

All non-teneral male flies taken on the fly-round were hunger-staged, employing the simple system used by Nash (1937). Out of 1,340 non-teneral males caught

TABLE III.

The number of flies caught in each subsection in three-monthly periods (3 years' data combined).

Section	WHITE					BLUE						YELLOW			GREEN					
Subsection	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	10–11	11–12	12–13	13–14	14–15	15-16	16-17	17-18	18-19	19-20	Total
Early rains	84	38	48	46	36	50	39	37	50	34	48	77	73	78	47	75	61	42	58	1021
Middle rains	67	50	64	70	61	35	11	40	33	24	56	76	41	66	65	56	33	35	81	964
Late rains	50	38	47	51	63	25	19	24	25	20	52	38	40	32	17	30	27	22	48	668
Dry season	28	35	28	42	30	29	25	11	23	12	19	47	33	33	35	28	18	16	49	541
Total ..	229	161	187	209	190	139	94	112	131	90	175	238	187	209	164	189	139	115	236	3194

over three years, 14 per cent. were hungry; the mean monthly figure ranged from 8 to 22 per cent. The comparable mean monthly figures for northern Nigeria, based on records for six years, ranged from 24 to 43 per cent. In the humid southern conditions presumably *G. palpalis* does not require food so often, and therefore fewer hungry flies are likely to be encountered. However, it must be mentioned that game is believed to be far more plentiful in the south, but, as will be shown below, there is as yet no evidence to indicate that *G. palpalis* makes much use of this source of food.

The data from Ugbobigha have been carefully analysed to see whether hunger is greater at any particular season, but it would appear that although the percentage of hungry flies may vary from month to month, this variation is not related to season.

Food hosts available for G. palpalis.

During the three years, all spoor seen on the fly-round was recorded; it was most often seen in Green section, and least often in Blue. The commonest animals were:—

Bushbuck (*Tragelaphus scriptus*):	65 records of spoor, 1 animal seen.
Duiker (*Cephalophus maxwellii*), ,, (*Cephalophus rufilatus*), ,, (*Sylvicapra grimmia*):	42 records of spoor, 4 animals seen.
Red river hog (*Potamochoerus porcus*):	25 records of spoor.
Elephant (*Loxodonta africana*):	14 records of spoor (July–November only).

In northern Nigeria, *G. palpalis* takes most of its food from reptiles and man. The *Varanus* lizard, which is so common in the north, is exceedingly rare at Ugbobigha.

Trypanosome Infection Rate.

From October 1955 to December 1956, 1,635 examples of *G. palpalis* were dissected, and 34 (2·1%) showed mature infections; of these, 23 (or about two-thirds) belonged to the *Trypanosoma vivax* group, and 11 (about one-third) to the *T. congolense* group. No salivary gland infections were found. The infection rates and proportions of the two trypanosomes were identical for the 913 males and 722 females.

The very low over-all infection rate found in *G. palpalis* at Ugbobigha is surprising in view of the high rates found in all but one of the other five species of tsetse that have been dissected from this area, in which game is plentiful. It may well be that *G. palpalis* takes its food mainly from hosts that do not carry *T. vivax* and *T. congolense*. Unfortunately it has not been possible to obtain many gorged flies of this species to send for serological testing, but, of the seven meals so far identified, five are from man, 1 from a reptile and only one from an unidentified Bovid.

Reproduction of *G. palpalis*.

The temperature of the pupal environment.

Frequent searches were made for pupae, but few were found. This was to be expected as the fly population is low, and pupal deposition likely to be spread over a wide area in such a mild climate. During one year, 24 pupae were found in Yellow and Green sections in sandy soil on top of the stream-bank.

Since Burtt (1946) had demonstrated in East Africa the importance of high pupal temperature in facilitating the infection of *G. morsitans* Westw. with *T. rhodesiense*, and since this finding might be applicable to *G. palpalis* and *T.*

gambiense in West Africa where *T. gambiense* is the causal agent of human sleeping sickness, it seemed desirable to get some idea of the temperatures to which pupae are exposed in southern Nigeria; as sleeping sickness is unknown at Ugbobigha, such figures would be interesting to compare with those already procured near Kaduna, in northern Nigeria, where this disease used to be rife (Nash & Page, 1953).

Soil temperatures at a site on the Green section are given in Table IV.

TABLE IV.

The soil temperature taken at ½-in. depth at a site where pupae of *G. palpalis* were found, Ugbobigha (mean of data for 2 years, 1955–56).

Monthly Temperature	Month											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Mean maximum (°F.)	80·2	81·9	81·9	81·7	79·7	78·6	76·6	75·4	77·7	77·9	79·0	78·1
Mean minimum (°F.)	70·3	74·3	75·2	74·8	74·5	73·7	73·2	72·1	73·0	73·4	73·8	71·1
Mean (°F.) ..	75·2	78·1	78·5	78·3	77·1	76·2	74·9	73·7	75·4	75·6	76·4	74·6
Mean (°C.) ..	24·0	25·6	25·8	25·7	25·0	24·6	23·8	23·2	24·1	24·2	24·7	23·7

The mean monthly values of the maxima at ½-in. depth ranged from 84·0 to 74·8°F. (28·9–23·8°C.), of minima from 75·7 to 70·2°F. (24·3–21·2°C.), and of the average from 79·7 to 73·8°F. (26·5–23·2°C.). The coldest months, when the pupal period is likely to be extended, are July, August and December.

Near Kaduna, similar data were collected only in the dry season and early rains (when pupae can be found), and over a period of three years. For comparison, the mean monthly temperatures at ½-in. depth as found at Ugbobigha and at Kaduna are given below for the months of November to May inclusive.

	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
Ugbobigha	76·4	74·6	75·2	78·1	78·5	78·3	77·1
Kaduna	68·1	65·9	67·4	70·3	73·8	76·1	75·8

The pupal temperatures for these months are considerably lower at Kaduna, which is the exact reverse of what might have been expected had a high pupal temperature been necessary for the infection of *G. palpalis* with *T. gambiense*. The absence of sleeping sickness at Ugbobigha, and the general rarity of the disease in southern Nigeria, clearly cannot be attributed to the exposure of pupae to low temperatures; as will be described elsewhere, the explanation is believed to lie in the lack of close contact between man and fly in the south.

Examination of females for pregnancy.

Gordon & Davey (1930) demonstrated by dissection of females and examination for pregnancy that there was a complete cessation of breeding by *G. palpalis* during the heavy rains at Freetown, Sierra Leone (average annual rainfall *c.* 150 in.); Nash & Page (1953) showed that no cessation of breeding occurred at Kaduna (average annual rainfall 47 in.). It was of interest, therefore, to know the situation at Ugbobigha (average annual rainfall 72 in.).

Females of *G. palpalis* were collected along streams within a radius of six miles of the field station, but not from the fly-round stream, from November 1955 to

October 1957, inclusive, and dissected and examined for pregnancy; the expression 'pregnant' denotes the presence of an egg or a larva *in utero*. The results are shown in Table V.

There is no suggestion of any cessation of breeding during the months of heaviest rainfall, August and September.

TABLE V.

Monthly variations in the percentage of females of *G. palpalis* that are pregnant.

Month	1955–56		1956–57		1955–57 combined	
	No. dissected	Pregnant (%)	No. dissected	Pregnant (%)	No. dissected	Pregnant (%)
November	23	30	39	23	62	26
December	12	4	58	48	70	46
January	38	16	35	43	73	29
February	37	21	65	29	102	26
March	43	40	21	24	64	34
April	57	33	19	31	76	32
May	78	29	51	26	129	28
June	71	34	36	27	107	32
July	51	40	43	42	94	40
August	51	10	46	28	97	19
September	36	28	53	38	89	34
October	36	28	41	34	77	31

Of the 1,040 females dissected, 31 per cent. were pregnant; this is very different from the figures found at Kaduna, where, out of 5,545 females dissected, 75 per cent. were pregnant. There was no difference in the technique of dissection, which was carried out by the same technician at both places, and all dissections were checked by an entomologist. There was, however, a difference in collecting technique, in that the flies at Kaduna were dropped into spirit immediately they were caught, lest abortion should take place before dissection. This technique could not be used at Ugbobigha, as the flies were also wanted for infection rate dissection; they were, however, dissected within 24 hours of being caught. It is possible, therefore, that many of the flies aborted before dissection (although there was no evidence of this) and that the pregnancy figures were thereby lowered. If, however, these figures correctly represent the pregnancy rate amongst wild females of *G. palpalis*, the slow rate of breeding implied must be a major cause of the low population levels usually found in southern Nigeria.

Of the 1,040 females dissected, 3·6 per cent. were virgin; this agrees closely with the figure of 4 per cent. found at Kaduna.

The Diurnal Activity Rhythm of *G. palpalis*.

To discover at what time of day *G. palpalis* is most active, catching was carried out from 7 a.m. to 7 p.m. daily (except Sundays) at a watering place on the River Ediovukor; all flies coming to the catchers were marked and released. Readings of temperature and humidity were taken at half-hourly intervals for possible correlation with any rhythm that might be found. To determine if there were any differences in activity in the dry season and the rains, the experiments were carried out on 23 days in January 1955, on 24 days in June 1955 and on 16 days in June 1954.

The results are shown in fig. 4. The total flies caught in each hour of the day during the course of an experiment have been expressed as a percentage of the

total flies caught during that experiment. In June 1954, 572 flies were caught, 1,006 in June 1955, and 490 in January 1955.

At both seasons of the year activity increases steadily between 7 and 10.30 a.m., and falls steadily between 3.30 p.m. and dusk; peak densities occur at different times between noon and 3.30 p.m.

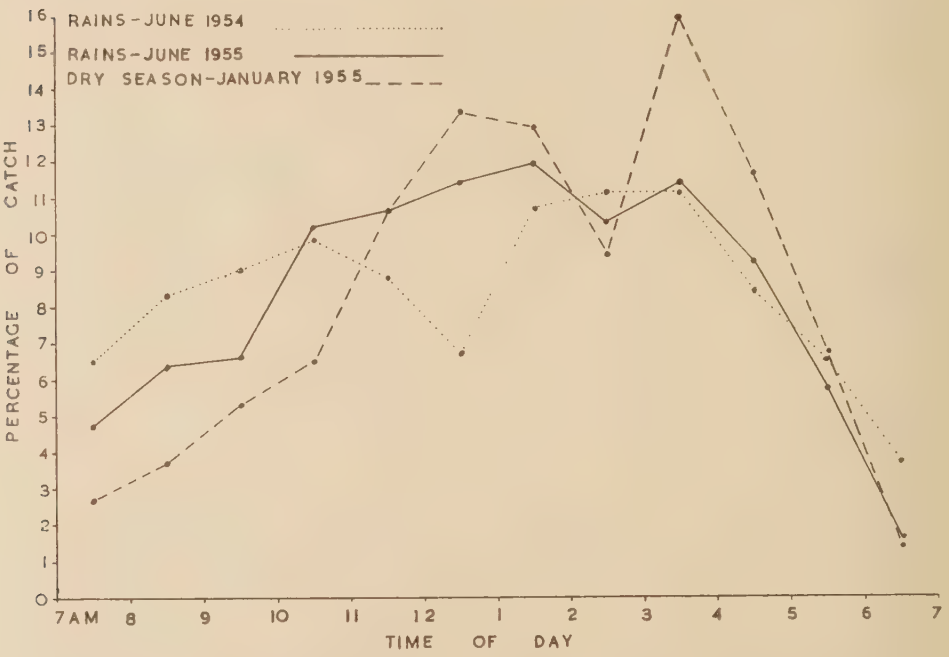


Fig. 4.—The hourly distribution of the day's catch, in three experiments, expressed as a percentage of the total flies caught during each experiment.

It is believed that the flies become active as the temperature rises in the mornings. It will have been noted from fig. 4 that the percentage of the day's catch of flies taken between 7 a.m. and 11 a.m. was least in the January 1955 experiment and greatest in the June 1954 experiment; Table VI shows that the temperature was lowest in the first-mentioned experiment and highest in the third.

TABLE VI.

Percentage of day's catch taken in each hour between 7 a.m. and 11 a.m., followed by temperature during that hour (in brackets, °F.).

	Hour				
	7–8	8–9	9–10	10–11	7–11
Jan. 1955	2·7 (69·4)	3·7 (72·5)	5·3 (75·9)	6·5 (79·7)	18·2
June 1955	4·7 (73·4)	6·4 (75·2)	6·6 (77·2)	10·2 (79·2)	27·9
June 1954	6·5 (74·5)	8·2 (76·6)	9·0 (78·6)	9·8 (80·4)	33·5

TABLE VII.

The effect of weather conditions upon the number of flies caught.

Weather conditions	7–10 a.m.			10 a.m.–1 p.m.			1–4 p.m.			4–7 p.m.		
	No. of flies	No. of ½ hours	Av. flies per ½ hr.	No. of flies	No. of ½ hours	Av. flies per ½ hr.	No. of flies	No. of ½ hours	Av. flies per ½ hr.	No. of flies	No. of ½ hours	Av. flies per ½ hr.
Sunshine ..	25	19	1·3	67	27	2·5	127	52	2·4	50	41	1·2
Intermittent sun	85	71	1·2	233	99	2·4	122	50	2·4	45	37	1·2
Overcast ..	67	48	1·4	10	7	1·4*	66	28	2·4	48	44	1·1
Rain	3	6	0·5	11	11	1·0	18	14	1·3	12	22	0·5

* Based on only 7 observations.

Although the decrease in activity between 3.30 p.m. and dusk (fig. 4) was associated in all three experiments with falling temperature, this is unlikely to be the cause of the decline in activity, since by 7 p.m. it had fallen only to 75–77°F.; and the cessation of activity between 6 and 7 p.m. is due, not to the flies' being inactivated by low temperature, but to the onset of darkness.

The total hours of sunshine do not appear to have much effect on activity. For example, on one day in June 1955, when there were 9½ hours of sunshine, only 31 flies were caught, but on another day, with only 4 hours of sunshine, 53 were taken; the best day's catch was 62 flies, made on a day with 3½ hours of sunshine, 5 hours of intermittent sunshine, 3 hours of overcast weather, and half an hour of rain. An analysis of the flies caught under various weather conditions, hour by hour throughout the day, was made for June 1955. The data have been compressed into three-hourly periods, and are shown in Table VII. Evidently, at all hours of the daytime, the flies are just as active when the weather is overcast as in full sunshine, but the effect of rain is to reduce activity by more than half.

Summary.

A population of *Glossina palpalis* (R.-D.) was studied for three years, between February 1954 and January 1957, at Ugbobigha, on the northern edge of the main rain-forest belt of southern Nigeria. A fly-round was laid out along the banks of a forested stream, running northwards from the forest belt into the savannah woodland, and was divided into four sections representing farmland, wide fringing forest, narrow fringing forest, and the edge of forest.

No major seasonal movements of the fly population from one section to another could be detected; it was found that open farmland and the edge of forest with good visibility always yielded the highest catches, whereas catches inside dense forest were always low. Data from other sources showed that at all seasons of the year *G. palpalis* may be found in small numbers throughout the savannah woodland, even in the absence of water. This species also occurs in very small numbers within the main forest belt, and in village clearings lying within this belt.

Apart from an increase in the second and third months of the rains (March–April) and a fall during the fourth and fifth months, the population tends to remain steady at a low level throughout the year. The increase in population is associated with a mean temperature of 79–80°F. (26·1–26·7°C.) and an average saturation deficit of 5·5 mb. These figures agree closely with those found to be optimal for *G. palpalis* by other workers. The decrease in population is associated with a falling temperature, but more especially with a mean saturation deficit that has dropped below 3 mb. These results agree closely with those found near the northern limit of the range of the species in Nigeria. The favourable period for increase during the wet season lasts for four months in northern Nigeria, but only two at Ugbobigha: this is believed to account for the much lower fly density found in the humid south.

Dissections of females showed no seasonal trend in the proportion that were pregnant, nor any cessation of breeding in the heavy rains (August–September). Of 3,130 flies caught, 45·5 per cent. were females, and of the 1,040 females dissected, only 3·6 per cent. were found to be virgin; in northern Nigeria, the comparable figures were 49·1 and 4·0 per cent., respectively. At Ugbobigha, there is no seasonal trend in the percentage of females amongst flies appearing to man. Among the non-teneral males caught, the mean monthly proportion that was hungry ranged from 8 to 22 per cent., but showed no seasonal trend, whereas comparable figures from northern Nigeria ranged from 24 to 43 per cent.; this suggests that *G. palpalis* requires food less often in the humid conditions of Ugbobigha, or possibly that game is more numerous.

Of 1,635 examples of *G. palpalis* dissected, 2·1 per cent. were found to have mature infections of trypanosomes; of the latter, about two-thirds belonged to the

Trypanosoma vivax group and about one-third to the *T. congolense* group. There was no difference in the infection rates of males and females.

Very few pupae were found, owing to the low fly population and the extensiveness of the breeding sites under the equable climatic conditions. The temperature of the pupal environment is considerably higher here than in northern Nigeria.

The diurnal rhythm of activity of *G. palpalis* was investigated both in the dry season and the wet. In both, activity increases steadily between 7 and 10.30 a.m., as the temperature rises, and falls steadily between 3.30 p.m. and dusk; peak activity occurs at various times between noon and 3.30 p.m. The numbers caught before 11 a.m., expressed as a percentage of the day's catch, increases at seasons when the temperature is higher. The flies are equally active in overcast weather and full sunshine, but rain reduces activity by more than a half.

Acknowledgements.

I wish to thank Dr. A. M. Jordan for supervising the pregnancy dissections of *G. palpalis* during March to October 1957, and Dr. T. A. M. Nash, C.M.G., Director of the West African Institute of Trypanosomiasis Research, for his advice and encouragement.

References.

Burtt, E. (1946). Incubation of tsetse pupae: increased transmission rate of *Trypanosoma rhodesiense* in *Glossina morsitans*.—*Ann. trop. Med. Parasit.* **40** pp. 18–28.

Geigy, R. (1948). Élevage de *Glossina palpalis*.—*Acta trop.* **5** pp. 201–218.

Gordon, R. M. & Davey, T. H. (1930). An account of trypanosomiasis at the Cape Lighthouse Peninsula, Sierra Leone.—*Ann. trop. Med. Parasit.* **24** pp. 289–318.

Nash, T. A. M. (1937). Climate, the vital factor in the ecology of *Glossina*.—*Bull. ent. Res.* **28** pp. 75–127.

Nash, T. A. M. & Page, W. A. (1953). The ecology of *Glossina palpalis* in northern Nigeria.—*Trans. R. ent. Soc. Lond.* **104** pp. 71–169.

Nash, T. A. M., Page, W. A., Jordan, A. M. & Petana, W. (1959). The breeding of *Glossina palpalis* in the laboratory for experimental work.—*7th Mtg int. sci. Comm. Tryp. Res., Brussels 1958* (in press).

Page, W. A. (1959). The ecology of *Glossina longipalpis* Wied. in southern Nigeria.—*Bull. ent. Res.* **50** pp. 595–615.

© Commonwealth Agricultural Bureaux, 1959.

SOME OBSERVATIONS ON THE *FUSCA* GROUP OF TSETSE FLIES (*GLOSSINA*) IN THE SOUTH OF NIGERIA.

By W. A. Page *

Research Entomologist, West African Institute for Trypanosomiasis Research, Kaduna, Nigeria.

Until recently, no studies had been made on the ecology in West Africa of the group of species of *Glossina* related to *G. fusca* (Wlk.). Tsetse flies of this group very rarely appear to man, and this gave the impression that they are so rare as to be of no economic importance. It was not until Nash & Davey (1950) found, by searching tree trunks, that these tsetse were exceedingly common in a locality where they were thought to be rare, that it was realised that species of the *fusca* group might be of considerable economic importance; this possibility was strengthened when Nash (1952) found a heavy infection rate with trypanosomes amongst a small sample of flies collected in the same locality.

Four out of the six species of the *fusca* group represented in Nigeria occur near the field station of the West African Institute for Trypanosomiasis Research at Ugbobigha, thus providing an excellent opportunity of doing some preliminary work on their ecology and economic importance.

Description of Area.

The situation and a general description of the field station has been given elsewhere (Page, 1959). The work on the species of the *fusca* group was undertaken 2–3 miles south of the station, where the edge of the Ishan plateau slopes gently to the savannah plain. The area (fig. 1), which is covered with tropical rain-forest (Keay, 1953), is intersected by the Umese, a small permanent stream, which runs in a steep-sided ravine some 40 ft. deep, as does the so-called sawpit stream to the south of it; it is bounded on the north by savannah, towards the east by the road leading to Ugbobigha and on the south by the steep-sided valleys of the small River Oruellen and the smaller sawpit stream. The vegetation is typical of the secondary forest found in southern Nigeria.

The Species of Tsetse present.

In this forest, *G. fusca* and two other members of the group, *G. tabaniformis* Westw. and *G. nigrofusca* Newst., were found, as well as *G. palpalis* (R.-D.) and *G. pallicera* Big. *G. medicorum* Aust., the fourth species of the *fusca* group in the district, does not occur in this thick forest.† *G. tabaniformis* was by far the commonest species, being some five times as numerous as *G. fusca*. *G. nigrofusca* was originally fairly common, but has been scarce of recent years.

Identification of species.

When an ecological study of a group of tsetse is envisaged, it is desirable to be able to identify the flies and subsequently release them. In the case of the *fusca* group, this presents some difficulty since, although genitalia dissection in the laboratory is a certain and simple method of identification, it necessitates

* Now at Dept. of Zoology, Sub-Dept. of Entomology & Parasitology, University of Edinburgh.

† The other two species of the *fusca* group that occur in Nigeria, but not in this district, are *G. haningtoni* Newst. & Evans and *G. nashi* Potts.

killing the insects, and this may reduce the population and precludes the use of fly-marking techniques. The existing keys using external characters are unreliable in many cases, and far too difficult for use in the field by junior staff. Buxton (1955) gives a Regional Key for West Africa. He separates *G. fusca* and *G. nigrofusca* from *G. tabaniformis* by the relative length of the palps and rightly points out that this is often a difficult character to apply. This meant that some other more obvious characters had to be found.

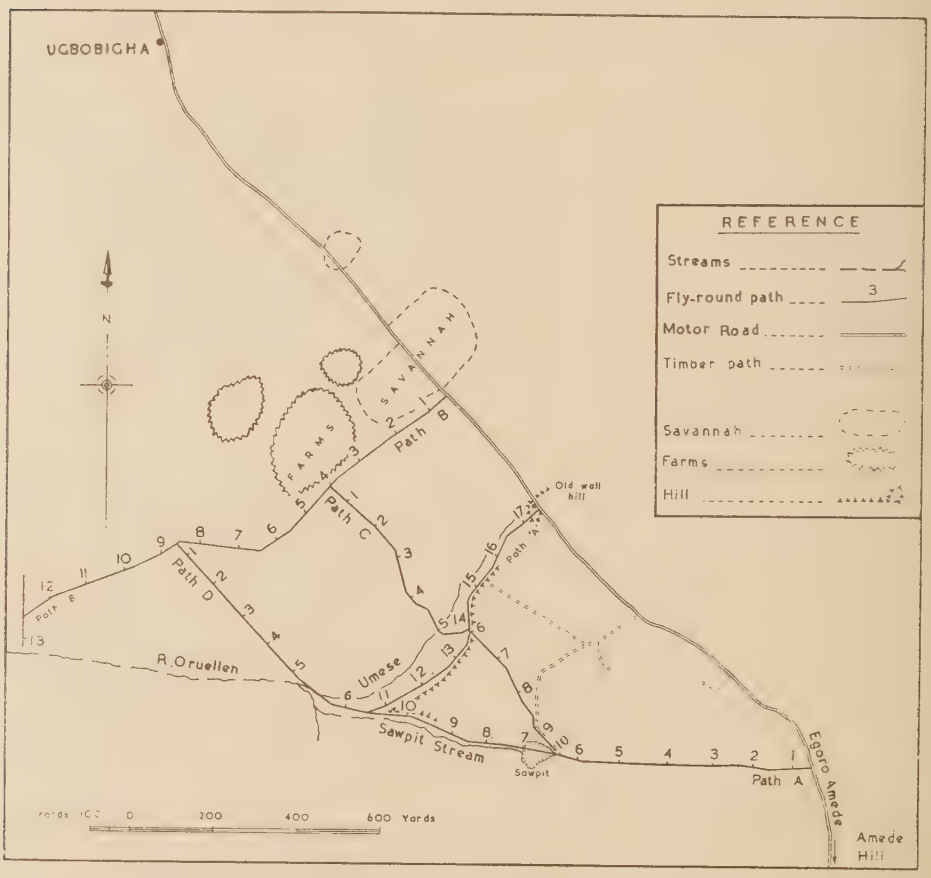


Fig. 1.—The area of the fly-round at Ugbobigha, in southern Nigeria, in which the ecology of the species of the *fusca* group was investigated. The fly-round consisted of four paths, each divided into a number of 100-yd. subsections (A 1–17; B 1–13; C 1–10; D 1–6).

It proved fairly simple to identify *G. nigrofusca* and *G. medicorum*, but difficult to separate *G. fusca* and *G. tabaniformis*; no simple method of distinguishing between the females of the last two species could be found, other than by dissection.

G. nigrofusca is a large, black fly, and can readily be distinguished from the other three species by the long fringe of the 3rd antennal segment, and by the black band found on both hind and mid-tibiae. Other species may show a darkening, which in some specimens is definite enough to be called a band, on

the hind tibiae, but in none have I seen a band or dark spot on both hind and mid-tibiae.

G. medicorum can be separated from the remaining two species by the absence of the blue-black spot on the sternopleuron, between the coxae of the fore- and mid-leg; this spot is very pronounced in *G. tabaniformis* and *G. fusca*.

The males of *G. tabaniformis* and *G. fusca* may be distinguished by the difference in colour of the hectors and hypopygium. In *G. tabaniformis*, these structures are dark brown or black; in *G. fusca* they are light brown in colour, being only very slightly darker than the abdomen; the hypopygium in some specimens is fairly dark, but this accentuates the paleness of the hectors. As regards the females, it should be possible to separate them by relative length of palps and length of antennal fringe, but I have never found determination of these characters simple enough to be completely reliable, even under primitive laboratory conditions, let alone in the field.

It should be pointed out that the above findings are based on live specimens, collected in this one locality.

The following is a simple key for the identification of these flies:—

1.	Large, black fly with pronounced antennal fringe about $\frac{3}{4}$ width of 3rd antennal segment; a black band on tibiae of both mid- and hind legs	*G. nigrofusca*
	Not as above	2
2.	No blue spot on sternopleuron	*G. medicorum*
	Blue spot on sternopleuron	3
3.	*Males.* Hectors and hypopygium light brown to cream ...	*G. fusca*
	Hectors and hypopygium dark brown to black	*G. tabaniformis*
	Females	*G. fusca* or *G. tabaniformis*

Man as Host.

So rarely do flies of the *fusca* group bite man or even appear to him, that it is possible to walk through forest and be entirely unaware of their presence, even though they may be there in large numbers. The villagers, at our request, would bring in the occasional flies that had bitten them. A record was kept, which after $3\frac{1}{2}$ years had reached a total of 58 flies, and gave the following information as to time of attack:—

6.30—10 a.m.	13
10 a.m.—noon	6
Noon—2 p.m.	1
2—4 p.m.	4
4—6.30 p.m.	16
6.30—10 p.m.	9
10 p.m.—6.30 a.m.	9

It will be noticed that most flies were caught in the first part of the morning and the latter part of the afternoon, and very few from noon until 2 p.m. This could give the impression that flies are crepuscular in habit, but this idea would be wrong, as will be shown later. The flies taken at night were caught by men hunting with lamps; these flies may have been activated by the light, or by disturbance of the vegetation. The flies usually bit the host on the leg or foot. On two occasions, flies bit men sleeping in their houses during the late afternoon, and on four occasions outside their houses in the village. One man was bitten at 10 p.m. on a moonlit night, whilst sitting by a fire, with his sheep and goats between him and the forest, which was about 50 yd. away. One specimen (*G.*

fusca) was caught by a man at the top of a palm tree, some 35 ft. in height. The above records refer to all four species, but *G. fusca* formed about half the total and *G. tabaniformis* nearly one-third.

Catches from searching Tree Trunks.

The tree-trunk searching technique proved invaluable whilst looking for a site for the field station; this survey covered Ondo and Benin Provinces of the Western Region of Nigeria. The results of collecting resting flies are given in Tables I and II, because they show that the work done by Nash & Davey (1950) in one place is applicable to other forest areas; further, whereas their work was done mainly in Forest Department plantations, the present surveys were made in natural forest of various ages.

TABLE I.

Resting position of tsetse.

Species	Sex	No.	Percentage of flies resting in given position			Percentage of flies resting with head downwards
			Vertical	Oblique	Horizontal	
G. fusca ..	♀	25	88	8	4	100
	♂	27	74	15	11	100
	Total	52	81	12	7	100
G. tabaniformis	♀	24	83	8	8	91
	♂	31	65	23	13	100
	Total	55	73	16	11	96
G. nigrofusca ..	Total	24	67	25	8	96

It will be seen that the majority of flies rest in a vertical position, with the head downwards. A certain number are found in an oblique position—this means that the branch upon which they were resting was oblique, not that the fly was sitting across the branch; similarly, the horizontal position means that flies were at rest on horizontal branches; in other words, the flies all rest parallel to the long axis of the branch upon which they are resting. Many of the oblique positions were only a few degrees from the vertical. Males show a tendency to be more irregular than females in their resting habits.

TABLE II.

Resting height of tsetse.

	G. fusca			*G. tabaniformis*			*G. nigrofusca*		
Height (ft.)	♂	♀	Total	♂	♀	Total	♂	♀	Total
0–3 ..	10	6	16	8	8	16	2	11	13
4–6 ..	15	15	30	18	13	31	4	4	8
7–9 ..	2	4	6	4	2	6	0	0	0
10–12 ..	0	0	0	1	1	2	1	2	3

Both *G. fusca* and *G. tabaniformis* appear to rest at heights between 4 and 6 ft. This is about man's eye-level, at which flies may be more likely to be seen and caught than if they were resting higher, although catchers are encouraged to look from bottom to top of a tree. Against this is the fact that *G. nigrofusca* apparently rests lower, more specimens being taken at 0–3 than at 4–6 ft. Most flies were resting on trees or creeper stems of 1- to 2-in. diameter. None was caught on trees of diameter bigger than 5 in.

As this technique was so useful when surveying an area, it was decided to see if it could be used to study the ecology of the fly in more detail, but the attempt was a failure, as too few flies were caught to enable any deductions to be made.

Catches using Bait-animals.

As reported in the W.A.I.T.R. Annual Report 1955 (Nash, 1956), a live red river hog (*Potamochoerus porcus*) was found in a trap in the forest in June 1955. In 35 minutes, 46 tsetse of the *fusca* group were caught on it. As the red river hog is obviously an attractive host, it was hoped that a domestic pig would also be attractive; a pig of the local breed, which is small, black and hairy, was therefore taken on several occasions to the forest, but only one example of *G. fusca* and one of *G. pallicera* came to it.

A white Zebu bull was also tried as bait, and proved very attractive to *G. fusca* and *G. tabaniformis*; regular fly-rounds at approximately weekly intervals were therefore begun in October 1955, using the bull as bait. A start was made by measuring five 100-yd. subsections along Path A (see fig. 1), which ran from the road down to a dell, where sawpits had been dug; the forest near the dell was much denser than that nearer the road. These subsections were numbered 1–5. As previous catches with the bait-ox had been made in the late morning, the first catch along the five subsections was made between 9.40 and 11.15 a.m. Only three flies were caught. It was decided to see if evening catches would be more successful, and, a week later, a catch was made between 5.15 and 6.50 p.m. (nightfall). Forty-two flies were caught, and so catches were continued in the evenings at weekly intervals. Results are shown in Table III.

TABLE III.

Catches of tsetse of the *fusca* group in 500 yd. of forest.

Month	1st round	2nd round	3rd round	4th round	Total
1955					
October	3*	42	95	104	244
November ..	73	4	13	12	102
December ..	6	12	35	—	53
1956					
January ..	14	14	9	11	48
February ..	1	5	11	14	31
March	8	2	4	0	14
April	10	5	15*	30*	60

* Catch made in the morning; all others made in the evening.

The total monthly catches decreased between October and March, which might be expected, since this covers the dry season, but in view of the erratic variation in numbers from week to week, the fly-round was subsequently extended,

until, by the end of July, it consisted of four paths (A, B, C and D), totalling 4,600 yd., and covering a good variety of vegetation and physical features. The layout is shown in fig. 1. This round gave more consistent results; one path was patrolled in each week, so that one full round was completed every month, and this was continued from August 1956 to July 1957.

Catching was carried out in the mornings, since the path was now too long to be traversed in the evening, and catches in the morning during the last two weeks of April had been satisfactory. In the centre of each subsection a suitable tree was marked, and the vegetation cleared around it for a distance of 10 ft., to give sufficient working area. The herdsman led the bait-bull along the path, and tied it to the marked tree. All flies resting on it and on the surrounding vegetation were caught. If there were no flies, or only a few, the team moved on after five minutes; otherwise the move was made when all the flies had been caught. The catching team, of five men, consisted of three catchers (left side, right side and back of bull), one fly handler, and one recorder. The flies caught were all taken to the laboratory to be dissected for trypanosomes, and, where appropriate, for species identification and examination for pregnancy. Readings were taken with a whirling psychrometer at each stopping place, and give some idea of the temperature and humidity in the forest in the forenoon, when the catches were made. The average value recorded on each round is shown in Table IV.

TABLE IV.

Temperatures and humidities recorded on the fly-round.

	Temperature (°F.)					Relative humidity (%)				
Path	A	B	C	D	Average	A	B	C	D	Average
1956										
September	—	—	—	76·5	76·5	—	—	—	95	95
October ..	76·1	—	77·7	79·0	77·2	96	—	96	90	94
November	79·2	75·6	79·2	79·3	78·3	93	94	90	91	92
December	72·3	76·5	74·3	80·1	74·8	95	94	79	88	89
1957										
January ..	72·0	77·0	81·1	78·4	76·1	60	64	84	87	74
February	78·4	84·2	81·7	81·5	81·1	70	81	83	86	80
March ..	81·1	80·1	81·0	80·6	80·6	82	77	82	75	79
April ..	81·1	80·6	80·4	80·2	80·6	76	87	94	88	86
May ..	76·1	81·7	77·7	79·0	78·6	96	89	92	91	92
June ..	79·7	75·7	76·6	76·5	77·7	87	92	94	95	92
July ..	78·3	78·6	79·7	—	78·8	87	90	86	—	88

Each reading shown under A, B, C and D is the average of readings taken at each stopping place during the one patrol per month on that path.

With the limited data available it is not possible to come to any conclusion as to the differences in temperature and humidity between the various parts of the forest, which is naturally so humid, and insulated by vegetation, that little variation would be expected to occur; there were indications that the humidity is slightly higher near the streams in the dry season, when some defoliation of the forest takes place.

Catch Results of *G. tabaniformis*.

As already mentioned, *G. tabaniformis* was by far the commonest species, representing 83 per cent. of the total catch. The fluctuations in monthly catches of this species are shown in Table V.

Catches were large in August and September 1956, at the height of the rains, and then decreased to a very low figure in February 1957, the end of the dry season. After this, they rose gradually, but had not, by July 1957, approached those of the previous August.

It is thought that the February 1957 figure was unusually low. In the previous year, 1956, when catches from the bait-bull were being made over 500 yd. of fly-round, 14 examples of *G. tabaniformis* were caught in February in 4 rounds,

TABLE V.

Catches of *G. tabaniformis*.

Month	Total flies	Percentage of females
1956		
August	423	57
September ..	453	49
October	332	57
November	123	55
December	148*	51
1957		
January	56	59
February	15	40
March	36	39
April	25	60
May	46	59
June	54	46
July	68	52

* Three inches of rain fell in this normally dry month.

or an average of 0·7 flies per round per 100 yd. In February 1957, the figure over the same subsections was 0·2 examples of *G. tabaniformis* per round per 100 yd.; over the whole round, the figure was 0·33 flies per 100 yd. This seems to indicate that the figures for February 1957 were abnormally low, and so led to the low figures for July 1957. The harmattan in January 1957 was more severe than is usual in those parts, and this may have affected the flies. The mean minimum relative humidity in the savannah in February 1957 was 43 per cent., as against the average for that month in 1954–56 of 56 per cent.; although the difference would not be as great in the forest, *G. tabaniformis*, being a forest dweller, is probably more susceptible to lower humidities than species that live in the savannah.

The population decrease may have been exaggerated by the killing necessary for identification of the flies caught, but it may be concluded that *G. tabaniformis* shows a peak population in the late rains, and a minimal population at the end of the dry season.

Of all the examples of *G. tabaniformis* caught, 56 per cent. were females (Table V). There was a considerable variation from subsection to subsection and from month to month, but no definite trend.

Variation in catches between the subsections.

There is considerable variation between the numbers of flies caught in the different subsections. In subsection B1, for example, which is near the savannah and the road, only nine flies (4 ♂♂, 5 ♀♀) were caught in a year; in subsection B13, on the bank of the R. Oruellen, 97 flies (34 ♂♂, 63 ♀♀) were caught.

An attempt was made to analyse the differences in vegetation. The forest is

nearly all of a secondary nature, having been farmed at various times over the past 80 years; the only places comparatively undisturbed are on the sloping banks of the stream. Each 100-yd. subsection was graded according to the density of the top, middle and lower strata, each having three degrees of density, A, B and C, according to the following criteria:—

Degree of density	Top stratum	Middle and lower strata
	Emergents	Canopy
A	Absent	Absent
B	Scanty	Broken
C	Plentiful	Closed

Of the 27 grades that could theoretically be found, 11 could be recognised in the area. They are shown in Table VI, together with the total flies caught per 100 yd. in each grade during the year.

TABLE VI.

The catches of *G. tabaniformis* in various grades of vegetation.

Density of vegetation			Subsections in each grade		No. flies per year per 100 yd.
Upper stratum	Middle stratum	Lower stratum	Path and number	Total no. of 100-yd. subsections	
C	C	A	B13	1	97
*A	A	B	C6, D6	2	65
B	C	A	B12	1	50
A	B	A	B9–11, D3	4	46
C	B	B	A3–8, C10, D4	8	41
A	B	C	B6–8, A11	4	38
B	C	B	A9, 10, 12, 13, C5, C8	6	34
B	B	C	A1, A2	2	31
B	B	B	A16–17, C1–4, D1–2, D5	9	31
A	B	B	B1–5, C7, C9	7	22
*A	A	B	A14–15	2	15

* Two distinct levels of catch were obtained in this vegetation type.

The method of grading was satisfactory, in that the catches in each 100 yd. of like forest were similar, with the exception of grade AAB (starred in Table VI), where two subsections (A14 and 15) produced 17 and 14 flies, respectively, and two other subsections (C6 and D6) produced 43 and 88 flies, respectively. It was felt that to put all these subsections together would be misleading, and so they have been separated into two groups.

Table VI shows that, apart from type AAB, the three biggest catches were made in forest where there is no lower-stratum canopy (types CCA, BCA, ABA). The largest catches are in CCA, which represents the only portion of primary forest in the area. It was situated at the top of the bank of the R. Oruellen; the visibility at this point was excellent, there were few shrubs and herbs, and it was possible to look right down to the river, some 50 ft. below, and across to the opposite bank, some 200 yd. away. The next largest catches were in type BCA, which differed only in that there were fewer tall trees, and more shrubs; but, in

spite of these small differences, the catches in this subsection were only just over half of those in the subsection of pure forest. The forest in subsections B9–11 of grade ABA was of about 10–15 years' growth, with a large number of young oil palms (*Elaeis guineënsis*), which gave the appearance of the plantation and suppressed the undergrowth beneath them; where there were no palms, there were dense tangles of shrubs and climbers, but these were small in area and consequently did not restrict visibility to any great degree.

In all the remaining grades, the lower stratum was present, with shrubbery and thicket tangles, so that visibility was restricted. It can be concluded that the fly favours parts of the forest where there is good visibility under a canopy of various heights and thickness.

No satisfactory explanation can be provided of the fact that of the four subsections graded as AAB, two gave very low, and two very high, catches. Presumably, in these subsections, factors other than vegetation are of over-riding importance, but from the evidence available it is not possible to identify these factors.

Catch Results of *G. fusca*.

The catches of *G. fusca* during the year (310 specimens) were much smaller than those of *G. tabaniformis* (1,679). The monthly catches are shown in Table VII, together with the percentage of females.

TABLE VII.

Catches of *G. fusca*.

Month	Total flies	Percentage of females
August	62	44
September	59	63
October	47	57
November	26	31
December	26	50
January	9	11
February	14	43
March	12	25
April	9	33
May	17	29
June	17	35
July	12	75

The highest catches were in August and September, at the height of the rains; catches then fell, reaching a minimum in January, and then varied haphazardly, with little sign of the increase that could be expected with the onset of the rains, and it is possible that this reduction in population is due to the killing of the flies caught. Females comprised 47 per cent. of the total catch, a lower figure than that obtained for *G. tabaniformis*, but still high.

Vegetational preferences.

The catches of *G. fusca* made in the various grades of vegetation already described and used in examination of the catches of *G. tabaniformis* are shown in Table VIII.

The largest catches of *G. fusca* were made in the same grade of forest as were those of *G. tabaniformis*. The lowest catches were in subsections B1–5, where

the path runs alongside savannah and farms. Why this should be so is not known; the reason is hardly likely to be a vegetational or climatic factor, since *G. fusca* is found in forest islands in the savannah. The grade AAB, which with *G. tabaniformis* showed two distinct sizes of catch, did not show this distinction with *G. fusca*, all catches in this grade being low. The catch in C6 was lower than in A14 and A15; and the catch in D6, although higher, was not proportionally so high as it was in the case of *G. tabaniformis*.

TABLE VIII.

Catches of *G. fusca* in various grades of vegetation.

Density of vegetation			No. flies per year per 100 yd.
Upper stratum	Middle stratum	Lower stratum	
C	C	A	17
B	C	A	10
A	B	A	9
C	B	B	8
A	B	C	8
B	B	C	8
B	C	B	7
B	B	B	5
A	A	B	5
A	B	B	2

Catch Results of *G. nigrofusca*.

Only 23 examples of this species (21 ♂♂, 2 ♀♀) were taken with the bait-bull during the year, or 1·1 per cent. of the total catch. These low numbers were rather surprising, since it was believed that *G. nigrofusca* was more numerous than *G. fusca*. In June 1955, a catch off the bait-bull of 81 flies of the *G. fusca* group had consisted of 35 specimens of *G. tabaniformis*, 27 of *G. nigrofusca* and 19 of *G. fusca*. Tree-trunk searching in early 1955 gave an overwhelming preponderance of *G. nigrofusca*, 24 out of a total of 27 flies being of this species, and although *G. nigrofusca*, being a large, dark fly, is perhaps more easily seen resting than are the other species, it would be unlikely to form such a large part of the catch if it were not present in good numbers. Either the population must have declined greatly in 1956 and 1957, or else the technique used was not suited to the habits of *G. nigrofusca*. It should be noted that of the 24 flies caught on tree trunks in 1955, 16 were female, whereas on the bait-bull only 2 out of 23 flies were of this sex.

Catch Results of *G. medicorum*.

As has been stated, *G. medicorum* did not occur in this forest; it did, however, occur about 5–6 miles to the north, in forest islands in the savannah. Specimens were found resting there, and also came in small numbers (1 or 2 caught per month) to the bait-ox used on the fly-rounds in the investigation of the ecology of *G. longipalpis* (Page, 1959). Pupae of *G. medicorum* were also found under logs in the forest islands together with those of *G. longipalpis*.

G. medicorum was also found in the forest bordering the R. Oruellen where it flowed through the savannah. This riverine forest was continuous with the forest where the *G. fusca* fly-round was done, so that *G. medicorum* could reach the main forest belt if necessary; as it did not do so, the rain-forest cannot be a

preferred habitat of this species. Nash & Davey (1950) made observations on this fly at Olokemeji near Ibadan, and state that although the area consists mainly of high, mixed deciduous forest, the woodland savannah is never far distant. It appears, therefore, that this fly prefers a slightly drier environment than *G. tabaniformis*. *G. fusca* seems to frequent a wider range of environments than *G. medicorum*, being found in association with the latter in the savannah and riverine forest and with *G. tabaniformis* in the main forest.

Infection Rate.

Differences of infection rates in various species.

Dissections of flies of the *fusca* group were carried out to determine their relative importance as carriers of trypanosomes. The results are shown in Table IX.

TABLE IX.

Infection rate in flies of the *fusca* group at Ugbobigha.

Species	No. dissected	No. positive	Percentage positive	*T. vivax* group		*T. congolense* group	
				No.	As % of infected flies of the species	No.	As % of infected flies of the species
G. tabaniformis	2380	89*	3·7	49	55	39	44
G. fusca ..	579	86*	14·9	66	77	19	22
G. nigrofusca	105	28	26·7	23	82	5	18
G. medicorum	91	14	15·4	14	100	0	0

* Includes one infection with *T. brucei* group.

The infection rates of the four species are very different, and the differences in distribution of the groups of trypanosomes are also quite marked. All the infections in the 91 specimens of *G. medicorum* examined were of the *vivax* group; Nash (1952) dissected 50 specimens of *G. medicorum* at Olokemeji and found seven flies infected, three with *vivax* group and four with *congolense* group.

These differences between *G. tabaniformis*, *G. fusca* and *G. nigrofusca* are even more striking when it is remembered that they were all caught in the same area of forest, under similar climatic conditions, and had the same choice of host. Possibly the different species select different hosts. Precipitin tests carried out by Mr. Weitz, of the Lister Institute of Preventive Medicine, Elstree, Herts., showed that of 35 specimens of *G. tabaniformis* examined, 21 (60%) had fed on red river hog (*Potamochoerus porcus*) and 8 (23%) on porcupine (*Atherurus africanus*).

Differences in infection rate in male and female flies.

In Table X are shown the infection rates in each sex of the four species.

The numbers of specimens of *G. nigrofusca* and *G. medicorum* are small, and no valid conclusions can be drawn from them. For both *G. tabaniformis* and *G. fusca*, however, a comparison of the infection rates in males and females shows the latter to be the higher (Table X), which, if members of the *fusca* group behave in a similar manner to other tsetse, and the females have a longer life, would be expected.

Buxton (1955) suggests that differences in the infection rates of the sexes

may be caused by sampling errors, young females of some species of tsetse being caught preferentially. These catches of *G. tabaniformis* and *G. fusca* on a bull show a high female infection rate. They also show a high percentage of females in the catch, indicating a more representative sample of the population than is the case when the percentage of females in the catch is low. The female percentage in catches of *G. morsitans* in Nigeria with man as bait is generally of the

TABLE X.

The infection rates of each sex of four members of the *fusca* group.

Species	Males				Females			
	Number dissected	% infected	% of infections due to group of		Number dissected	% infected	% of infections due to group of	
			T. vivax	*T. congolense*			*T. vivax*	*T. congolense*
G. tabaniformis	930	2·3	38	62	1450	4·7*	60	38
G. fusca ..	330	*11·5	71	26	249	19·3	81	19
G. nigrofusca ..	82	26·9	77	23	23	26·0	100	0
G. medicorum ..	54	11·1	100	0	37	21·3	100	0

* Includes one infection with *T. brucei* group.

order of 10–20 per cent. only, and the female infection rate is lower than in males; at W.A.I.T.R., dissections of 1,505 females and 12,757 males of *G. morsitans* showed infection rates of 1·7 and 3·4 per cent., respectively. These differences lend support to Buxton's view, and suggest that an explanation of the lower infection rate often observed in females may be due to a tendency to catch young (and hence non-infected) females preferentially.

It will be seen also from Table X that there is a tendency for infections with the *vivax* group to be greater in females than in males. This is very obvious in the case of females of *G. tabaniformis* where infections by the *vivax* group are nearly twice as many as those by the *congolense* group, whereas in the males, the reverse is true.

Economic Importance of the Species of the *G. fusca* Group.

It would appear that *G. tabaniformis* is not of great economic importance, since this species shows a low infection rate, and is confined to the forest, where cattle would not be kept. *G. fusca* and *G. medicorum* are of greater economic importance, since their infection rate is high, and they penetrate into the savannah by using forest islands and riverine vegetation as bases. *G. nigrofusca*, which is very heavily infected, and thus potentially most dangerous, is, at Ugbobigha, confined to the forest; elsewhere, as in Ghana, it comes out into the savannah (Nash, 1948) and is there likely to be of very great veterinary importance.

Examination of Females of *G. tabaniformis* for Pregnancy.

All the female flies captured were dissected for identification, and a note was made of the uterine contents at the same time.

From November 1955 to April 1956, 978 females of *G. tabaniformis* were dissected; of these, 42 (4·3%) had empty spermathecae. Of the remaining 936,

341 (36%) had an egg *in utero*, and 426 (46%) had a larva *in utero*, so that 82 per cent. of the females were pregnant.

Some of the numbers dissected in a month were small, so, in Table XI, figures have been added together in 3-monthly periods. There appears to be no fluctuation in the pregnancy rate during the year.

TABLE XI.

The percentage of females of *G. tabaniformis* that are pregnant.

Period	No. of fertilised females dissected	Females with egg or larva *in utero*	
		No.	%
Nov. 1955—Jan. 1956 ..	46	30	66
Feb.—Apr. 1956	147	115	78
May—July 1956	116	98	84
Aug.—Oct. 1956	426	358	84
Nov. 1956—Jan. 1957 ..	172	143	83
Feb.—Apr. 1957	29	23	79

These figures for *G. tabaniformis* are similar to those found in northern Nigeria for *G. palpalis* (Nash & Page, 1953) and suggest that no great differences from other species of tsetse are likely in the reproductive cycle of *G. tabaniformis*.

It is perhaps worth recording the following:—At 9 a.m. one morning, a female of *G. tabaniformis* was taken from a Bruce box and put into a tube; in this tube it deposited a black-lobed larva, which pupated. The mouth-parts and salivary gland of the fly were then dissected; no trypanosomes were found, and the headless body was returned to the tube, to await dissection for identification and pregnancy. This dissection was done at 10 a.m., and an egg was found in the uterus; so, within an hour, the larva had been extruded, and a new egg passed down into the uterus. Another female deposited a larva sometime between 9 a.m. and 12 noon, and by 12.15 p.m. there was an egg in the uterus. If in nature the period that the uterus is empty is only one to three hours, then one would expect to find about 98 per cent. of flies pregnant. This is not so, and it seems possible therefore that the decapitation of the fly leads to lack of nervous control of the ovary, with the consequent rapid ovulation of the egg. This agrees with Roubaud's view, quoted by Mellanby (1937), that ovulation in *Glossina* is not mechanical, but is controlled by the nervous system.

Summary.

Observations were made on *Glossina tabaniformis* Westw., *G. fusca* (Wlk.), *G. nigrofusca* Newst. and *G. medicorum* Aust., which all occur near the field station of the West African Institute for Trypanosomiasis Research at Ugbobigha in southern Nigeria. Identification of these species by the use of external characters has not been found possible between the females of *G. tabaniformis* and *G. fusca*, but is fairly simple between males of these two species and between both sexes of *G. nigrofusca* and *G. medicorum*. A simple key, based on external characters, is given. When necessary, females of *G. tabaniformis* and *G. fusca* were separated by dissection. *G. tabaniformis*, *G. fusca* and *G. nigrofusca* usually rest in a vertical position, with the head downwards, at a height of 4–6 ft. above ground (possibly lower for *G. nigrofusca*), on tree trunks, climber stems, etc., having a diameter of 5 in. or less.

A fly-round was started using a Zebu bull as bait. *G. tabaniformis* and *G. fusca* were caught in good numbers, *G. tabaniformis* forming 83 per cent. of the catch. There appears to be a decrease in population in the late dry season

(January and February) in both these species. Females comprised 56 per cent. of the total catch of *G. tabaniformis* and 47 per cent. of that of *G. fusca*.

The vegetation of the fly-round, which is typical secondary rain-forest as found in southern Nigeria, was analysed; both *G. tabaniformis* and *G. fusca* prefer old forest with an absence of a lower stratum, beneath a continuous middle stratum and good upper stratum, that is to say, where visibility beneath the trees is good. *G. nigrofusca* comprised only 1·1 per cent. of the catch on the fly-round, although at first it was believed to be common in the area. *G. medicorum* does not inhabit the main forest belt, but is confined to riverine vegetation and forest islands in savannah.

G. tabaniformis is unlikely to be of economic importance, since the rate of infection with trypanosomes is low (3·7%) and this fly is confined to the forest. *G. fusca* and *G. medicorum* are both of economic importance, since their infection rates are high (14·9 and 15·4%, respectively) and they travel out into the savannah grassland. *G. nigrofusca* has a yet higher infection rate (26·7%), but it is confined to the forest at Ugbobigha; where, as in Ghana, it frequents the savannah, it is potentially dangerous. Females of *G. tabaniformis* and *G. fusca* are more heavily infected than males.

Females of *G. tabaniformis* were examined (by dissection) for pregnancy; 82 per cent. of the females were pregnant and 4·3 per cent. unfertilised. No seasonal fluctuations in the rate were apparent.

Acknowledgements.

My thanks are due to Mr. Jonathan Mba for his invaluable assistance in this work; to Dr. Jordan for supervising the fly-rounds from March to July 1957, and to Dr. T. A. M. Nash, C.M.G., Director of the West African Institute for Trypanosomiasis Research for his suggestions and advice on the work.

References.

Buxton, P. A. (1955). The natural history of tsetse flies. An account of the biology of the genus *Glossina* (Diptera).—*Mem. Lond. Sch. Hyg. trop. Med.* no. 10, 816 pp. London, H. K. Lewis.

Keay, R. W. J. (1953). An outline of Nigerian vegetation.—2nd edn., 55 pp. Lagos, Govt. Printer.

Mellanby, H. (1937). Experimental work on reproduction in the tsetse fly, *Glossina palpalis*.—*Parasitology* **29** pp. 131–141.

Nash, T. A. M. (1948). Tsetse flies in British West Africa.—77 pp. [London] Colon. Off.

Nash, T. A. M. (1952). Some observations on resting tsetse-fly populations, and evidence that *Glossina medicorum* is a carrier of trypanosomes.—*Bull. ent. Res.* **43** pp. 33–42.

Nash, T. A. M. (1956). West African Institute for Trypanosomiasis Research. Annual report of the year 1955.—46 pp. Kaduna, Nigeria.

Nash, T. A. M. & Davey, J. T. (1950). The resting habits of *Glossina medicorum*, *G. fusca* and *G. longipalpis*.—*Bull. ent. Res.* **41** pp. 153–157.

Nash, T. A. M. & Page, W. A. (1953). The ecology of *Glossina palpalis* in northern Nigeria.—*Trans. R. ent. Soc. Lond.* **104** pp. 71–169.

Page, W. A. (1959). The ecology of *Glossina longipalpis* Wied. in southern Nigeria.—*Bull. ent. Res.* **50** pp. 595–615.

© Commonwealth Agricultural Bureaux, 1959.

BIONOMICS OF ANOPHELINE MOSQUITOS IN INLAND AREAS OF JAVA, WITH SPECIAL REFERENCE TO *ANOPHELES ACONITUS* DÖN.

By C. Y. Chow *

Entomologist, World Health Organization

R. Moh. Ibnoe

Acting Director, Malaria Institute Branch

and

Soejoed Tarko Josopoero

Assistant Malariologist, Office of Health Inspector, Surabaja, Indonesia.

Anopheles aconitus Dön. has long been known as an important vector of malaria in Indonesia (*e.g.*, Covell, 1944, p. 401); yet no systematic and thorough studies have been made on the bionomics of this species, although in a recent publication (Sundararaman, Soeroto & Siran, 1957) certain observations are recorded. Sundararaman, Soeroto & Siran (*loc. cit.*) showed that in the inland areas of Java, as distinct from the coastal regions where *A. sundaicus* (Rdnw.) is the chief vector of malaria, and from which *A. aconitus* is absent, the latter species is the principal, if not the only vector. The present study is therefore concerned with the bionomics of *A. aconitus*, particularly its resting and feeding habits, which are important for planning insecticide residual spraying. Data on other common Anopheline species have been collected at the same time.

The observations were carried out over a period of one complete year, from June 1957 to May 1958, in a village called Kebonsari and its vicinity on the border of Malang City, East Java. Another locality (Tjikeris, West Java, a hilly area) was chosen for observations, especially on *A. maculatus* Theo., regarded as an important malaria vector in hilly areas (Sundararaman, Soeroto & Siran, *loc. cit.*), also for a complete year, from April 1956 to March 1957. The above localities had not been sprayed with insecticides.

Seasonal Prevalence.

It is well known that rice-fields and irrigation channels are the main breeding places of *A. aconitus* (Sundararaman, Soeroto & Siran, *loc. cit.*), and that the highest larval population density occurs during a period of a few weeks before harvest. There are numerous rice-fields in and around Malang City, which yield two crops in a year: the harvest time for the first and more extensive crop is April–May and for the second crop, November–December.

As shown in Table I, *A. aconitus* occurs throughout the year, with the major peak in March–May and a minor peak in September–October. Seasonal incidence of *A. annularis* Wulp, which is also a rice-field breeder, is somewhat similar, but shows only one peak, in March. *A. vagus* Dön. is present in large numbers

* Now at WPRO, WHO, Manila.

throughout the year, with its peak in November–February, which is usually the rainy season. Other species, such as *A. kochi* Dön., *A. barbirostris* Wulp, *A. subpictus malayensis* Hack. and *A. tessellatus* Theo., were found in small numbers. *A. maculatus* Theo., which was only taken in the hilly area, showed no large difference in its monthly density (Table II).

Resting Habits.

Day-time resting places.

The density of all the above species found in a cattle-shed at night was much higher than in the same shed in the day-time. In most parts of Java, cattle-sheds

TABLE I.

Monthly density (per man-hour per station) of Anophelines caught at Malang City, East Java.

Species	1957						1958						Aver-
		June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	age
A. aconitus	(1)	24	24	33	86	94	44	54	35	63	133	82	166	70
	(2)	9	5	3	2	3	7	11	12	28	54	44	65	20
	(3)	6	1	1	2	2	1	1	0	1	1	4	2	2
	(4)	0	1	0	3	0	3	1	0	1	1	1	9	2
	(5)	30	17	3	5	17	—	—	—	—	—	39	53	23
A. annularis	(1)	18	5	18	59	22	17	14	53	60	168	35	20	41
	(2)	0	1	1	4	1	1	1	6	12	11	2	1	3
	(3)	0	1	0	1	1	0	1	1	0	0	1	0	1
	(4)	0	0	0	1	0	1	1	0	1	1	1	0	1
	(5)	0	1	1	0	0	—	—	—	—	—	0	0	0·3
A. barbirostris	(1)	4	4	21	15	3	1	2	1	1	2	1	2	5
	(2)	4	1	7	20	7	2	3	5	6	10	6	4	6
	(3)	0	7	3	2	3	3	4	0	0	0	1	1	2
	(4)	0	0	1	3	2	2	0	1	1	0	0	0	1
	(5)	0	0	0	1	0	—	—	—	—	—	0	1	0·3
A. kochi	(1)	9	31	21	5	7	1	7	26	9	24	9	22	14
	(2)	6	2	3	1	1	1	2	3	8	6	3	7	4
	(3)	7	1	0	0	0	0	1	0	0	0	0	1	1
	(4)	0	4	2	1	0	1	0	1	0	1	1	3	1
	(5)	1	1	3	2	1	—	—	—	—	—	2	1	1
A. subpictus malayensis	(1)	3	3	3	10	5	4	9	5	2	0	0	1	4
	(2)	1	1	1	1	1	1	4	2	1	0	0	1	1
	(3)	2	0	0	2	2	1	1	1	1	0	0	0	1
	(4)	0	0	0	2	0	0	0	1	0	0	0	0	0·3
	(5)	0	0	1	1	0	—	—	—	—	—	0	0	0·3
A. tessellatus	(1)	1	3	1	1	0	1	1	1	4	1	1	3	1·5
	(2)	0	0	0	0	1	0	1	1	1	1	0	1	1
	(3)	0	0	0	1	1	0	0	0	0	1	0	0	0·3
	(4)	0	0	0	0	0	0	0	0	0	1	1	0	0·2
	(5)	0	0	0	0	0	—	—	—	—	—	1	0	0·1
A. vagus	(1)	75	98	59	63	46	354	109	355	204	16	8	77	122
	(2)	56	50	15	10	4	47	91	85	34	8	5	9	35
	(3)	14	7	3	2	3	3	4	4	4	3	1	2	4
	(4)	14	10	12	5	2	8	15	10	6	3	1	2	7
	(5)	9	9	17	31	16	—	—	—	—	—	3	5	13

(1) in a single cattle-shed from 16 night collections, June 1957–May 1958; (2) in a cattle-shed; (3) in four houses, and (4) on ' salak ' plants, in the morning of 49 weekly collections, middle June 1957–May 1958, at Kebonsari, Malang; and (5) on river banks at Tandjungredjo, Malang. June–October 1957 and April–May 1958.

have no walls but only roofs. Usually very few or no mosquitos are present in such sheds during the day because of profuse light and ventilation. The data shown in Table I, however, are based on the studies of a cattle-shed with well-closed walls.

Very few mosquitos could be found in houses either during the day or at night. For the greater part of the year, only one or two examples of *A. aconitus* were caught per man-hour per house during the morning collections (Table I). Hardly any examples of *A. maculatus* were found in houses throughout the year.

Nevertheless, Anopheline mosquitos, particularly *A. aconitus* and *A. maculatus*, were prevalent in outdoor shelters. Many females of *A. aconitus* were observed resting in the day-time on the banks of streams, the density there being much higher than in the houses; a small number were also found underneath the leaves of the 'salak' plant (*Zalacca edulis*) (Table I.). Venhuis (1942) also reported that vegetation or moist and damp hollows in stream banks are the favourite day-time resting places of *A. aconitus*.

A high percentage (23%) of females of *A. aconitus* that rest outdoors in the day-time are freshly fed (Table III).

TABLE II.

Monthly density and density (per cent.) for each quarter in the night of *A. maculatus* and *A. aconitus* from night collections in cattle-shed and on palm and coffee plants, at Tjikeris, Purwakarta, West Java, April 1956–March 1957.

Month	*A. maculatus*		*A. aconitus*	
	Shed	Plants	Shed	Plants
1956				
Apr.	36	37	9	18
May	34	23	15	14
June	52	13	20	12
July	44	6	15	9
Aug.	50	3	8	17
Sept.	56	3	10	15
Oct.	68	15	2	18
Nov.	63	18	9	14
Dec.	17	11	5	17
1957				
Jan.	21	2	5	12
Feb.	27	2	4	12
Mar.	18	4	5	17
Percentage in each quarter of night :				
18–21 hr.	3	23	5	42
21–24 hr.	40	24	43	19
00–03 hr.	42	30	31	19
03–06 hr.	15	23	21	20

Two collectors catching for 15 minutes in each quarter from the beginning of the first hour of each quarter.

In Tjikeris, West Java, we found that palm and coffee plants were the favourite outdoor shelters in the day-time for both *A. aconitus* (average of 3·5 per man-hour) and *A. maculatus* (average of 2 per man-hour), the former species preferring palms and the latter coffee plants. In the night collections throughout

a year, a larger number of examples of *A. aconitus* were found on these plants than in cattle-sheds, the reverse being the case with *A. maculatus* (Table II).

Cattle-shed and window exit trap.

In order to see what percentage of mosquitos would remain in the cattle-shed after feeding and what percentage would leave before early morning, a more or less well-closed cattle-shed was selected at Kebonsari, Malang City, and equipped

TABLE III.

Abdominal condition of Anophelines caught from outdoor resting places on river banks at Tanjungredjo, Malang City.

Species	Total	Percentage of			
		FF	UF	HG	G
A. aconitus ..	1301	23	16	57	4
A. kochi	45	7	45	46	2
A. vagus	101	4	26	62	8

Total number from 18 morning collections in April–May 1958.
FF = fully fed; UF = unfed; HG = half-gravid; G = gravid.

with a window exit trap of the Muirhead-Thomson type. The shed housed five cows from 18 hr. throughout the entire night, during which time the window exit trap was kept open. At 07 hr., the following morning, the window trap was closed and the mosquitos inside it were collected: at the same time, two mosquito collectors, by the use of sucking tubes, made as complete a collection as possible of all the mosquitos remaining inside the shed. A senior malaria technician classified the abdominal condition of all the Anophelines taken from both the window trap and from the cattle-shed immediately after they had been collected. The results of 30 weekly morning collections are given in Table IV.

It will be seen that a large number of the mosquitos (all the six Anopheline species collected) were found in the window trap. Of a total of 6,602 examples of *A. aconitus* found, 56 per cent. escaped to the trap, the rest being taken in

TABLE IV.

Anophelines taken in window exit trap and remaining in a cattle-shed at Kebonsari, Malang City.

Species	Total number	Percentage in		In trap, percentage of				In shed, percentage of			
		trap	shed	FF	UF	HG	G	FF	UF	HG	G
A. aconitus	6602	56	44	59	5	34	2	49	6	42	3
A. annularis ..	3084	73	27	53	10	36	1	49	9	42	0
A. barbirostris ..	324	59	41	60	13	26	1	71	3	26	0
A. kochi	777	71	29	69	7	23	1	78	3	18	1
A. subpictus malayensis	189	60	40	50	8	37	5	42	14	44	0
A. vagus	10300	54	46	46	13	36	5	42	5	47	6

Total numbers caught in 30 weekly morning collections, October 1957–May 1958.

the shed. The results of the classification of the abdominal condition of the mosquitos remaining inside the shed and of those taken in the exit trap varied erratically from collection to collection, and hence no useful inference can be drawn. It would, however, seem that appreciable but variable numbers of fully fed females of *A. aconitus* will remain in cattle-sheds (when these have walls) during the day-time, when the blood-meal is under digestion and ova are under development.

Experimental hut and window exit traps.

Although the cattle-shed mentioned above was more or less well closed, it was quite probable that a certain number of the mosquitos escaped through holes, crevices, gaps under the eaves, etc. A well-closed experimental hut was therefore built with the same materials (bamboo mats) for walls and ceiling as were

TABLE V.

Recovery of Anophelines released overnight in an experimental hut. Numbers remaining in the hut and taken in the window exit traps on the following morning.

Species		Remaining in the hut	In window traps			Grand total
			East trap	West trap	Total	
A. aconitus	UF	1	10	1	11	12
	HG	42	55	39	94	136
	G	5	2	4	6	11
	Total	48	67	44	111	159
A. annularis	UF	1	2	3	5	6
	HG	3	7	6	13	16
	G	0	0	0	0	0
	Total	4	9	9	18	22
A. barbirostris	UF	0	0	0	0	0
	HG	19	19	21	40	59
	G	1	1	0	1	2
	Total	20	20	21	41	61
A. kochi	UF	0	1	2	3	3
	HG	51	18	13	31	82
	G	1	0	1	1	2
	Total	52	19	16	35	87
A. subpictus malayensis	UF	0	0	7	7	7
	HG	0	7	3	10	10
	G	0	0	1	1	1
	Total	0	7	11	18	18
A. tessellatus	HG	1	1	0	1	2
A. vagus	UF	2	3	8	11	13
	HG	28	67	32	99	127
	G	15	7	13	20	35
	Total	45	77	53	130	175
Grand total :		170	200	154	354	524

Five tests during November 1957 to May 1958 with a total of 1,500 wild-caught Anophelines (500 of which were *A. aconitus*).
Percentage of all species recovered: 35—Distribution: in hut, 11; in traps, 24.
Percentage of *A. aconitus* ,, : 32— ,, : ,, , 10; ,, , 22.

used in local houses and of more or less the same size. Two window exit traps were attached to the hut, one facing east and the other west.

In five tests, from November 1957 to May 1958, known numbers of mosquitos that had been collected in the morning from a cattle-shed or from an animal-baited trap and kept in cages and fed with sugar solution till 18 hr. were released into the hut. At the same time the window traps were set. A complete collection was made at 07 hr. the following day. In the five tests, 1,500 Anophelines (500 of which were of *A. aconitus*) were released, but only 35 per cent. (11% in the hut and 24% in the traps) of the mosquitos were recovered. Apparently the rest must have escaped during the night through the small interstices of the bamboo mats. Of the 500 examples of *A. aconitus* released, 159 (32%) were recovered, 10 per cent. inside the hut and 22 per cent. in the traps (Table V).

There was not much difference in the extent of attraction between the east- and west-window traps.

The observation that only very small numbers of *A. aconitus* are found in houses and in animal-sheds (without walls, the most common type) both inland and in the hilly area of Java, and the fact that in the above tests the majority of the females of *A. aconitus* escaped or attempted to escape from the building, provide further confirmation that this species is highly exophilic.

Feeding Habits.

Place and time of feeding on human bait.

The following test was made at intervals throughout the year. During the entire night (from 18 hr. to 06 hr.) one mosquito collector would make hourly collections, each lasting 15 minutes, during which catching would be made continuously of the mosquitos feeding on a boy, about 15 years old, sitting with bare arms and legs (without any protection from a mosquito net) just outside a house. The same would be done inside the house on the same night. As shown in Table VI, from 15 collections during the night (monthly or twice a month) throughout a full year from June 1957 to May 1958, a total of 44 examples of *A. aconitus* was caught inside the house as against 124 outside the house. This

TABLE VI.

Number of Anophelines taken biting human bait inside and outside a house.

Time (hr.)	*A. aconitus*		*A. annularis*		*A. barbirostris*		*A. kochi*		*A. vagus*	
	In	Out	In	Out	In	Out	In	Out	In	Out
18–19	0	3	0	0	0	0	0	0	9	2
19–20	2	19	0	0	2	0	0	0	13	2
20–21	5	28	0	1	15	0	3	0	13	12
21–22	7	15	1	3	7	0	1	2	24	20
22–23	2	23	1	5	7	1	6	2	26	17
23–24	5	7	2	1	2	0	3	1	26	12
00–01	5	3	1	1	1	1	7	1	24	14
01–02	10	14	2	1	1	2	2	0	22	2
02–03	5	7	0	1	2	1	1	0	17	2
03–04	2	3	1	2	2	2	0	0	16	1
04–05	0	2	0	0	2	0	0	1	10	2
05–06	1	0	0	0	0	0	0	0	27	1
Total	44	124	8	15	41	7	23	7	227	87

Total number from hourly catches (15 minutes each hour) of 15 night collections throughout a year, June 1957–May 1958, by one collector from one human bait in each situation at Kebonsari, Malang City.

TABLE VII.

Time of feeding of *A. aconitus* on cattle bait. Numbers and abdominal condition percentages of females taken in hourly catches from walls of a cattle-shed at Kebonsari, Malang City.

Time (hr.)	Total number		Abdominal condition (%)			
			Fully fed	Unfed	Half-gravid	Gravid
18–19	354		31	16	45	8
19–20	467		31	37	27	5
20–21	389		45	27	23	5
21–22	403		55	22	19	4
22–23	508		69	10	17	4
23–24	616		67	8	21	4
00–01	760		75	6	16	3
01–02	603		78	5	13	4
02–03	659		78	3	14	5
03–04	571		75	3	19	3
04–05	548		67	3	22	8
05–06	448		68	6	22	4
Total	6326	Weighted mean percentages	65	10	20	5

Totals for 16 night collections (once or twice a month) between June 1957 and May 1958, made by two collectors operating for 15 minutes from beginning of each hour.

TABLE VIII.

Time of feeding of other Anopheline species on cattle bait. Numbers and percentage fully fed of females taken in hourly catches.

Time (hr.)	*A. annularis*		*A. barbirostris*		*A. kochi*		*A. subpictus malayensis*		*A. tessellatus*		*A. vagus*	
	No.	FF (%)	No.	FF (%)	No.	FF (%)	No.	FF (%)	No.	FF (%)	No.	FF (%)
18–19	42	17	72	60	61	48	63	30	16	50	601	30
19–20	112	44	67	55	142	60	57	30	10	60	1123	50
20–21	154	58	46	85	109	73	50	46	9	33	893	46
21–22	196	45	17	77	145	76	15	20	9	78	965	40
22–23	313	55	37	92	97	87	31	40	6	50	869	48
23–24	275	62	29	91	137	76	34	20	8	100	782	48
00–01	380	64	40	80	118	83	18	55	8	62	841	56
01–02	407	71	48	70	100	73	38	45	5	100	779	43
02–03	397	64	68	80	70	80	13	44	9	55	867	27
03–04	440	68	56	73	102	82	48	67	7	86	774	44
04–05	427	67	72	91	96	82	19	56	6	33	720	26
05–06	363	62	42	60	63	67	12	41	8	62	621	64
Totals and weighted mean percentages	3506	62	594	75	1240	75	423	41	101	63	9835	44

Other details as in Table VII.

shows that three times as many females of *A. aconitus* will feed on man outdoors (exophagous) as indoors (endophagous). On the other hand, in the same test. 227 examples of *A. vagus* were found biting man indoors as against 87 outdoors. The number of examples of other Anopheline species caught was too small for definite conclusions, although *A. barbirostris* and *A. kochi* showed a tendency toward endophagy.

As to the time of feeding, *A. aconitus* fed on man throughout the night; the outdoor feeding took place mostly before midnight.

Time of feeding in cattle-shed.

In the same way, collections during the entire night were made in the cattle-shed that housed five cows, but with two collectors to catch mosquitos from the walls and the lower portion of the roof. Amongst the large numbers of mosquitos collected, all seven local Anopheline species at Kebonsari, Malang City, and *A. maculatus* in West Java were found to feed on cattle throughout the night (Tables II, VII & VIII).

TABLE IX.

Results of precipitin tests on blood-meals of Anophelines collected at Malang City, Lamongan Regency and Djombang Regency, East Java, from June to August 1957 and March to May 1958.

Species	Source	Number tested	No. negative	No. positive with anti-sera					Percentage positive for human blood
				man	ox	goat	horse	mixed	
A. aconitus Dön.	shed	1026	4	4	1018	0	0	0	0·4
	house	5	0	2	3	0	0	0	2 out of 5
	joint dwelling	48	0	3	45	0	0	0	6·0
	outdoor	359	0	62	276	3	18	0	17·3
	Total	1438	4	71	1342	3	18	0	5·0
A. annularis Wulp	shed	500	0	0	500	0	0	0	0·0
	joint dwelling	12	0	1	11	0	0	0	1 out of 12
	outdoor	4	0	2	2	0	0	0	2 out of 4
	Total	516	0	3	513	0	0	0	0·6
A. barbirostris Wulp	shed	160	0	1	159	0	0	0	0·6
A. kochi Dön.	shed	352	0	0	352	0	0	0	0·0
A. subpictus malayensis Hack.	shed	369	0	1	368	0	0	0	0·3
	joint dwelling	25	0	1	24	0	0	0	1 out of 25
	Total	394	0	2	392	0	0	0	0·5
A. tessellatus Theo.	shed	28	0	0	28	0	0	0	0·0
A. nigerrimus Giles	shed	239	3	10	220	3	0	3	4·2
A. vagus Dön.	shed	675	1	0	671	2	0	1	0·0
	house	10	0	0	10	0	0	0	0·0
	joint dwelling	42	0	0	42	0	0	0	0·0
	outdoor	16	0	2	14	0	0	0	2 out of 16
	Total	743	1	2	737	2	0	1	0·3

Mosquitos collected from houses, cattle-sheds, joint dwellings and outdoors.

A. aconitus was found to feed on cattle comparatively more during the third quarter of the night (Table VII), *A. annularis* mostly after midnight, and the other species at varying hours of the night.

In another experiment the aim was the total collection of mosquitos, *i.e.*, an attempt was made by four to six collectors to catch all the mosquitos throughout every hour in the night, instead of two collectors catching for only 15 minutes in each hour. Two such collections during the entire night were undertaken, with similar results. Out of a total of 801 examples of *A. aconitus* caught during the whole night, 720 were fully fed, with the first peak at midnight to 01 hr. (142 fed) and the second peak at 04 to 05 hr. (132 fed).

Host preference.

Mosquito blood-meals were collected in the inland area and sent to the Lister Institute for Preventive Medicine, Elstree, Herts., England, for precipitin tests. The results, given in Table IX, show that all the local Anopheline species are highly zoophilic. Of a total of 1,438 examples of *A. aconitus* collected from cattle-sheds, houses, joint dwellings (dwellings occupied jointly by humans and cattle) and outdoors (mainly from river banks, a few from salak plants), only

TABLE X.

Numbers of Anophelines and time of entry into an animal-baited trap and of escape to a window trap fitted to a nearby cattle-shed at Kebonsari, Malang City.

Species	Totals and abdominal condition (%)	Time (hr.) of entry to animal-baited trap				Time (hr.) of escape to window trap			
		18–21	21–24	00–03	03–06	18–21	21–24	00–03	03–06
A. aconitus	Total	124	274	187	266	158	151	135	86
	FF	65	65	76	73	37	74	64	60
	UF	9	10	4	3	12	2	23	14
	HG	25	25	20	24	60	24	10	23
	G	1	0	0	0	1	0	3	3
A. annularis	Total	106	94	54	105	105	9	64	26
	FF	57	44	46	52	40	80	62	46
	UF	8	13	8	7	30	0	26	0
	HG	35	43	46	38	30	20	12	54
	G	0	0	0	3	0	0	0	0
A. barbirostris	Total	22	27	45	48	2	1	9	4
	FF	95	100	100	86	50	100	100	100
	UF	0	0	0	4	0	0	0	0
	HG	5	0	0	10	50	0	0	0
	G	0	0	0	0	0	0	0	0
A. kochi	Total	176	210	110	100	59	15	58	30
	FF	86	78	92	73	80	100	93	80
	UF	4	11	5	3	10	0	0	0
	HG	9	11	3	22	10	0	7	10
	G	1	0	0	2	0	0	0	10
A. vagus	Total	80	94	24	40	14	5	5	2
	FF	75	77	30	38	23	40	80	50
	UF	0	6	4	0	0	60	0	0
	HG	20	17	66	50	71	0	20	50
	G	5	0	0	12	6	0	0	0

Total number of mosquitos caught in three night collections in April–May 1958.

5·0 per cent. were positive for human blood. However, 17 per cent. of 359 examples of *A. aconitus* collected from outdoors had human blood. Of 48 of *A. aconitus* from joint dwellings, three were positive for human blood. Of the total from all situations (1,438), 93·5 per cent. were positive for ox. No blood-meals were collected in the hilly area, so there are no data for *A. maculatus*.

Time of Entry and Exit.

Entry into an animal-baited trap.

An animal-baited trap similar to the Magoon type, with calf as bait, was employed at Kebonsari, Malang City. The bait was put in for the whole night, from 18 hr. to 06 hr., being taken out only during the collections. Three tests throughout the night were made in April–May 1958, when *A. aconitus* was at the peak of its density. All the mosquitos were collected during the last hour of each quarter of the night. As shown in Table X, *A. aconitus* entered the trap in large numbers throughout the night, with peaks during the second and fourth quarters of the night; *A. kochi* and *A. vagus* entered in larger numbers before midnight. Details of exit-trap catches made in a nearby cattle-shed on the same dates are included in Table X. These are discussed on p. 657. The abdominal condition of all mosquitos taken in both these sets of catches is also shown in the table.

Entry into a cattle-shed.

Only one collection throughout the night was made, on 4th March 1958, also at the peak of *A. aconitus*, in a walled cattle-shed at Kebonsari, Malang City.

TABLE XI.

Numbers of Anophelines and time of entry into a cattle-shed and of escape to a window trap in each quarter of the night.

Species	Totals and abdominal condition (nos.)	Time of entry to cattle-shed					Time of escape to window trap				
		Quarter					Quarter				
		1st	2nd	3rd	4th	Total	1st	2nd	3rd	4th	Total
A. aconitus	Total	78	142	290	295	805	30	120	81	41	272
	FF	21	84	260	221	586	13	66	64	30	173
	UF	4	4	3	2	13	0	1	0	0	1
	HG	53	54	27	72	206	16	53	16	11	96
	G	0	0	0	0	0	1	0	1	0	2
A. annularis	Total	160	166	288	336	950	15	74	87	51	227
	FF	107	113	252	262	734	10	48	42	42	142
	UF	16	9	7	0	32	0	2	1	0	3
	HG	37	44	29	74	184	5	24	44	9	82
A. kochi	Total	4	16	17	12	49	0	9	8	5	22
	FF	3	13	16	12	44	0	9	8	5	22
	HG	1	3	1	0	5	0	0	0	0	0
A. vagus	Total	39	31	20	28	118	4	3	3	2	12
	FF	15	25	14	21	75	0	2	3	2	7
	UF	0	0	1	0	1	0	0	0	0	0
	HG	24	6	5	7	42	3	1	0	0	4
	G	0	0	0	0	0	1	0	0	0	1

On one night, 4th March 1958, at Kebonsari, Malang City.

Five cows were kept in the shed from 18 hr. throughout the whole night. As complete as possible a collection of mosquitos was made by six to eight collectors during the last hour of each quarter of the night. As may be seen from Table XI, more individuals of *A. aconitus* entered the shed as time passed. Details of exit-trap catches made in the same cattle-shed on the same night are included in Table XI. The relative numbers of mosquitos taken in these and in the shed are discussed below. The abdominal condition of all mosquitos taken in both these sets of catches is also shown in the table.

In West Java, *A. maculatus* and *A. aconitus* entered the cattle-sheds mostly during the second and third quarters of the night (Table II).

Exit into window traps.

Exit traps attached to the windows of houses for entire nights and operated weekly throughout the year (from June 1957 to May 1958) caught mosquitos only on four or five occasions, when one to three examples of *A. aconitus* were caught.

Exit traps attached to the windows of a cattle-shed and operated by day (from 07 hr. to 18 hr.) revealed only one to three examples of *A. aconitus* (mostly half-gravid) on each occasion. However, as mentioned above (p. 650 and Table IV), hundreds of mosquitos were caught in window exit traps at night (for the period from 18 hr. to 06 hr.). In order to know at what period of the night most of the mosquitos would try to leave, and how long they would remain indoors after feeding, observations were made in the following ways:

Collection from an exit trap every five minutes from 18 hr. to 06 hr.—On one night in December 1957 collections were made from an exit trap fixed to the window of a more or less well-closed cattle-shed at Kebonsari, Malang City. In each of the 144 collections made during this night, only one or two examples of *A. aconitus* were found. The disturbance to the window trap every five minutes presumably deterred the mosquitos from going into it. Hence these figures are of no real value.

Collection from an exit trap every half hour from 18 hr. to 06 hr.—In each of the 24 collections made during one night in October 1957, only one to six examples of *A. aconitus* (mostly fed) were caught, except in the first two collections, *i.e.*, from 1800 to 1830 hr., when there were 24 examples of *A. aconitus*, and from 1830 to 1900 hr., when there were 32, most of which were unfed and half-gravid. *A. annularis* showed the same tendency.

Collection from an exit trap every quarter of the night from 18 hr. to 06 hr.—Data for three nights in April–May 1958 show (Table X) that *A. aconitus* left a cattle-shed in decreasing numbers as the night progressed. Of 158 examples of *A. aconitus* that made their exit during the first quarter, 60 per cent. were half-gravid, 37 per cent. freshly fed, 2 per cent. unfed, and 1 per cent. fully gravid. In the case of *A. annularis*, the largest number made their exit during the first quarter of the night.

Collection from an exit trap at intervals between 18 hr. and 06 hr., combined with complete catch of resting mosquitos.—Observations were also made, on other occasions, on mosquitos caught inside the cattle-shed at various intervals, the window trap being searched at the same intervals.

The figures of numbers of mosquitos entering a cattle-shed, together with those of mosquitos taken concurrently in exit traps, provide information on the resting behaviour of mosquitos in a cattle-shed, the proportion of those entering during each interval that rest there, and the length of time for which they do so after feeding. The window trap was kept open for each quarter of the night from 18 hr. to 06 hr., while the mosquitos inside the cattle-shed were collected as completely as possible during the last hour of each quarter by six to eight collectors. As shown in Table XI, only 25 per cent. of the examples of *A.*

aconitus were caught in the exit trap. These observations show that a considerable number of individuals of *A. aconitus* rested on walls of the cattle-shed for at least two hours after feeding.

A. vagus remained in the cattle-shed much longer than *A. aconitus*, as only 9 per cent. of the former species were caught in the window trap.

Discussion and Conclusions.

The observations recorded here show that, in the areas studied, negligible numbers of *A. aconitus* could be found in houses during the day, and very few or none in typical cattle-sheds, which have no walls. In cattle-sheds that have walls, appreciable but variable numbers of fully fed individuals may remain during day-time, but larger numbers are to be found by day resting on the banks of streams and on the lower surface of leaves of shrubs. This is in agreement with the observations of Venhuis (1942) but not altogether with those of some other workers. For instance, Sundararaman, Soeroto & Siran (1957) recorded the density of *A. aconitus* in houses in Middle Java as 25 per man-hour in the day-time and 100 at night.

In view of the observation, in the present work, that nearly three times as many examples of *A. aconitus* bite man outdoors as indoors, and the finding of human blood in a considerable number of examples of this species that were collected from outdoor resting places, it seems that these individuals, after feeding outdoors, may remain in outdoor resting places. It is also possible that some individuals that have fed on man indoors may remain indoors for a time after feeding, leaving later for outdoor resting places. Observations in a walled cattle-shed near Malang City showed that many adults of *A. aconitus* remain inside the shed for at least two hours after feeding.

The extreme scarcity of *A. aconitus* in houses both by day and by night in the area where the present observations were made may be due to biological variation. These studies should, therefore, be repeated in different parts of the country.

The present observations show that, in general, *A. aconitus* is highly, though not exclusively, zoophilic in the areas studied and readily enters cattle-sheds to feed. Covell (1944) reported that this species appears to feed on man only where cattle are scarce. Walch (1932) and Sundararaman, Soeroto & Siran (1957) have recorded up to 60 per cent. of females of *A. aconitus* caught in houses in certain parts of Java to contain human blood. The feeding habits of the species, therefore, appear also to be variable.

It is not yet known what effect surfaces sprayed with DDT will have on populations of *A. aconitus*, since, judging from the present studies, many of the individuals that feed on man do so outdoors, and rest outdoors. It will, therefore, be necessary to undertake a careful study of the effect on a population of *A. aconitus* of a residual insecticide and the extent of any decline in the prevalence of malaria after its application. Later, it may be necessary to determine whether a residual insecticide would by itself bring about a complete interruption of transmission, despite the fact that a large proportion of the females of *A. aconitus* is exophilic.

In the two areas studied, *A. maculatus* was only taken in the hilly area in West Java. Nearly five times as many examples of this species as of *A. aconitus* were taken there over a period of a year in a cattle-shed at night, but negligible numbers were found in houses. It rests in vegetation both by day and by night. Over a thousand specimens of these two species from this area were dissected, but no malaria infection was found. Venhuis (1941) found infected specimens of *A. maculatus* during a malaria epidemic in East Java. Sporozoites were also found in a single example of *A. maculatus* out of 130 examined in the Kalikadjar area of Middle Java by Sundararaman, Soeroto & Siran (1957), but infection was also found in *A. aconitus* at the same time in that area. In many hilly areas,

especially where there are terraced rice-fields, *A. aconitus* and *A. maculatus* have been found together, just as in the present study in West Java, but the former species is usually present in larger numbers (Sundararaman, Soeroto & Siran, 1957). It may be that *A. maculatus* is of less importance than *A. aconitus* in malaria transmission. Its rôle needs further investigation.

The other species found are not important in malaria transmission (Sundararaman, Soeroto & Siran, 1957).

Summary.

Anopheles aconitus Dön. has long been known as an important vector of malaria in Indonesia. More recently it has been shown to be the principal, if not the only vector in the inland areas of Java. *A. maculatus* Theo. has been regarded as an important vector in hilly regions.

The observations recorded in the present paper were carried out in an inland area in East Java between June 1957 and May 1958, and in a hilly one in West Java between April 1956 and March 1957, and were concerned, in particular, with the resting and feeding habits of these two species in so far as they might influence methods of control.

A. aconitus is found in great numbers throughout the year with a major peak of density from March to May, about harvest time of the first and more extensive rice crop.

In the areas studied, *A. aconitus* is largely exophilic and, where man is concerned, exophagous, nearly three times as many examples being taken biting man outdoors as indoors, and 17 per cent. of 359 examples taken outdoors were positive for human blood as compared with 5 per cent. of 1,438 examples from all situations. Of the remainder, 93·5 per cent. were positive for ox. On the whole, therefore, this species is highly, though not exclusively, zoophilic and readily enters cattle-sheds, built of bamboo matting, to feed, and, in those sheds that have walls as well as roofs, up to 75 per cent. may remain for at least two hours after having fed, and appreciable but variable numbers of fully fed individuals may remain during day-time.

Most of the feeding on man outdoors took place before midnight, and, on cattle in sheds, between midnight and 0600 hr., with peaks between midnight and 0100 hr. and between 0400 and 0500 hr., respectively. Peak periods of entry into an animal-baited trap were during the second and fourth quarters of the night.

These results differ somewhat from those reported from certain other localities in Java by other workers. There is, therefore, a need for careful repetition, in other areas, of studies of the bionomics and for experiments on the effect on a population of *A. aconitus* of applications of a residual insecticide.

A. maculatus occurs in the hilly area in considerable numbers throughout the year, and there seems to be no great seasonal fluctuation. This species rests mainly on coffee and palm plants both by day and by night, but readily enters cattle-sheds at night. No blood-meals from this species were subjected to the precipitin test. It is suggested that the importance of *A. maculatus* in the transmission of malaria needs further investigation.

Over 1,000 examples of *A. maculatus* and *A. aconitus*, taken in the hilly area, were dissected, but no malaria infection was found.

A. vagus Dön. is present in the inland area in large numbers during the greater part of the year, with its peak from November to February, during the rainy season. It is more endophilic and endophagous than *A. aconitus* but is not considered important in malaria transmission.

A. annularis Wulp has its peak in March, and *A. kochi* Dön. in May. *A. barbirostris* Wulp, *A. subpictus malayensis* Hack. and *A. tessellatus* Theo.

were found only in small numbers. All these species are highly zoophilic in the areas studied; they are not considered important in malaria transmission.

Acknowledgements.

Thanks are due to the Government of Indonesia and to the World Health Organization for kind permission to publish this paper; to the Inspector of Health of East Java and to Dr. Moh. Imanoedin (Deputy Inspector of Health in charge of malaria control in East Java), to the Municipal Health Officer of Malang City and to the Residency Doctor of Djakarta for full co-operation and providing all necessary personnel and facilities; to Messrs. Sumantri and Soedjono (malaria technicians of Malang City) and to the malaria technicians of Regency Purwakarta (Residency Djakarta) for their technical assistance through the whole study in East Java and West Java, respectively; to Dr. D. K. Viswanathan, Senior Malaria Adviser for the WHO Regional Office for South East Asia, for valuable criticism of the manuscript; and to Mr. B. Weitz, of the Lister Institute of Preventive Medicine, Elstree, England, for the valuable contribution of the precipitin tests.

References.

Covell, G. (1944). Notes on the distribution, breeding places, adult habits and relation to malaria of the Anopheline mosquitoes of India and the Far East.—*J. Malar. Inst. India* **5** pp. 399–434.

Sundararaman, S., Soeroto, R. M. & Siran, M. (1957). Vectors of malaria in Mid-Java.—*Indian J. Malar.* **11** pp. 321–338.

Venhuis, W. G. (1941). De vindplaatsen van geinfecteerde *Anopheles maculatus* tijdens een epidemie in Oost-Java.—*Geneesk. Tijdschr. Ned.-Ind.* **81** pp. 2178–2188.

Venhuis, W. G. (1942). *Anopheles aconitus* aan kaliwanden.—*Geneesk. Tijdschr. Ned.-Ind.* **82** pp. 99–112.

Walch, E. W. (1932). Het verband tusschen de voorkeur van Nederlandsch-Indische Anophelinen voor menschen- of dierenbloed en haar gevaarlijkheid. (Tweede mededeeling.)—*Geneesk. Tijdschr. Ned.-Ind.* **72** pp. 682–709.

© Commonwealth Agricultural Bureaux, 1959.

NOTES ON GALL MIDGES (CECIDOMYIIDAE) ON NIGERIAN CROPS WITH A DESCRIPTION OF A NEW SPECIES OF *THOMASIELLA* RÜBSAAMEN.

By K. M. Harris, B.Sc.(Wales), D.T.A.(Trin.)

Entomologist, Department of Agricultural Research, Ibadan, Nigeria.

(Plate XVIII.)

Investigation of the gall midges of crops in Nigeria has revealed an undescribed species which causes sorghum stems to lodge and two species, one on rice, the other on benniseed (*Sesamum orientale*), which are known as pests of these crops in India.

The sorghum stem gall midge is here described and attention is drawn to the occurrence of *Pachydiplosis oryzae* (Wood-Mason) and *Asphondylia sesami* Felt both in Nigeria and in other parts of Africa.

Sorghum Stem Gall Midge.

In October 1956 my assistant, Mr. S. V. A. Ajomale, discovered Cecidomyiid larvae feeding in the stems of guineacorn (*Sorghum vulgare*) at the Regional Research Station, Zaria, Northern Nigeria.

Adults reared from these larvae obviously belong to the *Lasioptera* group of genera in the tribe Lasiopterariae, but their generic placing is a matter of some difficulty. The extent to which the *Lasioptera* complex should be split into separate genera has been a matter of debate for some years and the discovery on sorghum of a new gall midge aggravates the problem. In the keys of Kieffer (1913), Rübsaamen & Hedicke (1926–39) and Felt (1925) the sorghum stem gall midge falls into the genus *Prolasioptera* Rübs. In this genus and in *Hybolasioptera* Rübs. the hooks on the ovipositor are described as being on the upper lamella, but the sorghum stem gall midge has the hooks anterior to the upper lamella and in this respect shows affinity to the genus *Lasioptera* Meigen. Yet it differs from this genus in that the middle lamella of the male genitalia is entire, not emarginate, and in this respect agrees with Rübsaamen's diagnosis of the genus *Thomasiella*, a genus that contains several species whose larvae live in graminaceous stems.

Although the larvae of the sorghum stem gall midge are peculiar in having a 4-toothed anchor-process instead of the more usual bifid one, it is considered advisable to describe the midge as a new species of *Thomasiella* pending a revision of the Lasiopterariae.

Thomasiella sorghivora, sp. n.

Male. Length: 2·0–2·7 mm. Wing length: 2·2–2·4 mm. Eyes large, black, contiguous. Antennae 2 + 14 or 15; 1st segment obconic, rather long, twice as large as the second which is globular; 3rd and 4th coalescent, flagellar segments bead-like, sessile, about as wide as long at the base becoming progressively shorter and relatively wider, each with a basal and a distal whorl of curved setae and two relatively conspicuous rings of applied circumfila united to each other laterally by a thread; terminal segment often longer than preceding segments and bluntly

rounded distally. Palps triarticulate, short; 1st segment short, variable, square or subquadrate; 2nd segment longer, tapering slightly, bearing one long and a number of shorter setae distally; 3rd slightly longer than 2nd, tapering distally to a truncate tip, setose. Neck short. Thorax brown, mesonotum dark brown dorsally. Wings with 3rd vein close to and parallel to costa, joining costa in the distal $\frac{1}{3}$rd; costa, sub-costa and 3rd vein thickly scaled, fifth vein forked, indistinct. Halteres large, scaled. Legs with coxae and trochanters dark brown, other segments lighter; femora, tibiae and tarsi thickly scaled; 2nd tarsal segment at least 5 times length of the 1st, claws strongly curved with a small recurved tooth near base; empodium extending beyond claws. Abdomen brown, clothed in dark brown scales. Genitalia (fig. 1) with basal clasp segment almost three

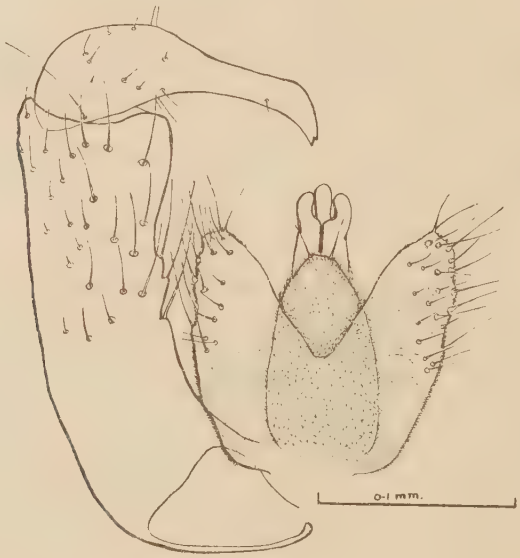


Fig. 1.—*T. sorghivora*, sp. n.: Male genitalia, dorsal view, with left clasper omitted.

times as long as broad, slightly curved, with strong setae along inner side and on dorsal distal surface; distal clasp segment stout at base and narrowing in distal half; upper lamella bi-lobed, pubescent; thickly setose along outer half of each lobe; lower lamella shorter than dorsal, entire and slightly truncate at distal end which bears a single pair of setae; pubescent. Style long, straight, smoothly rounded at apex, enclosed by the long ventral appendages; style and ventral appendages protruding beyond the ventral plate, but not as far as distal end of basal clasp segment.

Female. Length: 2·2–3·1 mm. Wing length: 2·1–2·4 mm. Antennae 2 + 14 or occasionally 15 segments. Abdomen orange, terga clothed with dark brown scales, ovipositor (fig. 2) one third of length of abdomen; the two rows of strong chitinous hooks extending dorsally for more than half length of last segment but not attaining terminal lobe; terminal lobe apically indented, setose; small ventral appendage finely setose. Otherwise much as in male.

Pupa. Length: 3–4 mm. At first flesh-coloured later becoming orange, with dark bands (of scales) on dorsal surface of abdomen. Cephalic horns ("armure cervicale") at base of antennal sheaths prominent, chitinised, bluntly pointed. Five pairs of abdominal spiracles, prominent, horn-shaped, sclerotised.

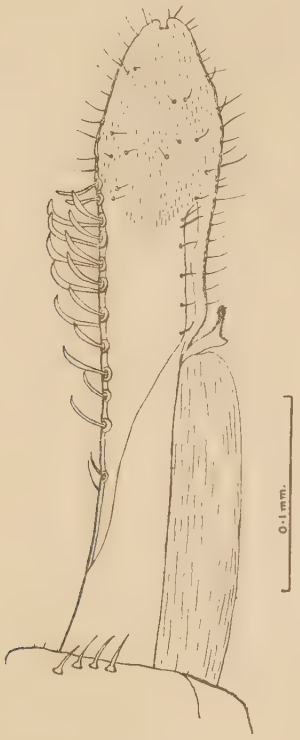


Fig. 2.—*T. sorghivora*, sp. n.: Ovipositor, left side.

Larva. Length attaining 3·5 mm. Creamy becoming orange-pink or orange with age. Body elongate and gradually widening anteriorly. Breast-bone (fig. 3) quadridentate, teeth heavily sclerotised; prominent lateral wings; shaft narrowing to basal bulb which is indented posteriorly.

Material. Northern Nigeria: Zaria, Zonkwa, Kano, Mokwa; Western Nigeria: Ibadan. Holotype male (Cecid. 13,236) and 10 males (Cecid. 11,298, 13,237, 13,229–35) (Barnes collection) and 105–6 and 111 (author's collection); 7 females (Cecid. 11,299, 13,238, 13,597–13,599 (Barnes collection) and 27, 103 and 112 (author's collection)); 4 pupae (11,300, 13,239 (Barnes collection), 108–10 and 115 (author's collection)), and several larvae (13,240–2 (Barnes collection) *et al.* in author's collection) reared from guineacorn (*Sorghum vulgare*). Holotype from Zaria deposited in Barnes collection, Rothamsted.

T. sorghivora has been reared from *Sorghum vulgare* at Samaru and Maigana near Zaria, Northern Nigeria and at Ibadan in Western Nigeria. In addition larvae and pupal cases have been found at Zonkwa, Kano and Mokwa, Northern Nigeria.

Observations on *T. sorghivora* have been largely confined to the environs of the Regional Research Station, Samaru, Zaria, where it was first discovered in 1956, and subsequently reappeared in 1957 and 1958. The locally-grown variety, " Farafara ", is attacked in September and October, during the fifth and sixth months of its growth. Colonies of larvae appear in the upper internodes of the head-bearing stem, usually just above a node, and eat out galleries within the stem.



Fig. 3.—*T. sorghivora*, sp. n.: Breastbone of larva.

The occurrence of larvae just above the node suggests that the eggs may be laid under the leaf sheath which would protect newly hatched larvae before they enter the stem. The larvae pupate within the stem and the adults emerge through holes to the exterior leaving the empty pupal skins protruding (Pl. XVIII, figs. 1–3). The stem is weakened and at harvest in November a high proportion of attacked stems may be lodged (Pl. XVIII, fig. 3). During November pupation ceases; the remaining larvae become inactive and remain so until the following growing season. These larvae survive in guineacorn stems which, after harvest, are generally collected and stored through the dry season for use in building and as fuel. Such stems provide an important reservoir for infestation of the new crop.

Loss of yield resulting from attacks by *T. sorghivora* has not been assessed but particularly severe lodging due to the midge occurred on an acre of guineacorn grown at Mokwa in 1958, and moderate damage to stems was seen at Maigana, near Zaria and Ibadan in the same year.

On the basis of observations to date, the writer considers the sorghum stem gall midge a minor pest of cultivated sorghums in Northern Nigeria.

Rice Stem Gall Midge (*Pachydiplosis oryzae* (**Wood-Mason**)).

In October 1956 a condition locally known as " whip " disease of rice (*Oryza sativa*) was recognised and reported by officers of the Department of Agriculture

from rice fields near Shendam, Northern Nigeria. Gall-midge larvae and pupae were found in affected plants and adults were reared from them.

Adults and pupae were compared with material of *Pachydiplosis oryzae* in the Barnes collection, comprising males and females from Kayo in the French Sudan; females and pupae from Masa in the Republic of the Sudan and females from Bihar, India, and proved to be conspecific.

In addition to the African records cited above, *P. oryzae* has been reported by Descamps (1956) from the French Cameroons and it is concluded that this midge, which is well known as a pest of rice in India and the Far East, is well established in the Sudan and Guinea zones of tropical Africa.

Since 1956, the rice stem gall midge has been collected from *O. sativa* at the Lowlands Experimental Farm, Shendam and at the Federal Rice Research Station, Badeggi. Affected plants produce galls which are elongate, green or yellow-green, hollow and completely round in cross section, giving the stem more the appearance of an onion leaf than a rice shoot. These hollow galls contain the larvae and pupae of the midge. Later they become twisted and the extremity of the gall falls over at the point where the adult has emerged, so giving the appearance of a whip. Shoots that have been attacked produce no head though heads may later be produced on tillers from the same plant.

In 1958, the midge appeared at Shendam and Badeggi early in the growing season in late July and early August. In one field at Badeggi almost every plant was attacked in early August but a month later these plants were growing strongly and few galls could be found. At Shendam the damage caused by the midge was not particularly severe either in 1956, the year of its discovery, or in subsequent years.

P. oryzae is not likely to be of major importance on well-grown rice where a single crop is grown during the season but may be of local importance in poor seasons or on experimental areas where more than one crop per season is grown.

Further information on this pest is given by Barnes (1956).

Benniseed Gall Midge (*Asphondylia sesami* Felt).

The benniseed gall midge or gingelly fly (*Asphondylia sesami*) is a pest of *Sesamum orientale* (benniseed, simsim or gingelly) in southern India and has also been recorded from this plant in Uganda and the Sudan.

In October 1956, midges were reared from *S. orientale* at Zaria, Northern Nigeria and in August 1958 at Mokwa. Males, females and empty pupal cases have been compared with material of *Asphondylia sesami* in the Barnes collection, comprising bred males from Kampala in Uganda, and Kadugli in the Sudan, and males and females from India. The Nigerian specimens were obviously conspecific.

In Nigeria, the benniseed gall midge has been recorded at Yandev, Mokwa and Shendam, but occurs also at Zaria, which is outside the main benniseed-growing area.

Experimental plots of benniseed have been severely attacked, particularly when a series of different sowings has been made or a number of varieties grown, and damage to farmers' late-planted crops has been reported in some years from Yandev. Benniseed plants are usually attacked in July and August, when in flower, though galled pods containing larvae and pupae have been collected from late-planted crops at Zaria in October and at Shendam in November.

When young flowers are attacked the galls often appear before the petals have been shed and the developing pod is swollen, distorted and useless. But if the pod is attacked later in its development the gall forms as a discrete swelling on the loculus and, although seed formation is depressed near the gall, other loculi of the same pod and other parts of the damaged loculus may still bear seed.

Each gall contains a single larva but there may be galls on more than one

loculus of the pod and more than one gall on each loculus. The larva pupates within the gall and the adult emerges through an exit hole leaving the empty pupal case protruding.

Hymenoptera were reared from field collections of galled pods at Yandev, Shendam and Zaria in such large numbers as to suggest that natural parasitism was at a high level. The parasite complex has not been closely studied, but among the Hymenoptera reared and identified the following may be parasites of the midge: *Neanastatus africanus* Ferrière, *Eurytoma* sp., a genus near *Aniso-pteromalus*, and two undetermined genera, one a Eulophid and the other a Pteromalid.

Further information on this pest is given by Barnes (1949).

Acknowledgements.

My thanks are due to Dr. J. M. Waterston, Director of Agricultural Research, Ibadan, for his general interest in this work; to the Department of Agriculture, Northern Nigeria, for provision of facilities at Zaria and for the co-operation of officers in the field; and to the Director of Rothamsted Experimental Station and Dr. K. Mellanby, the Head of the Entomology Department, who have provided facilities for me to study during my vacation leave. I am especially grateful to Dr. H. F. Barnes who has placed at my disposal his collection, library and experience.

The Hymenoptera reared from galled benniseed pods were identified by the Commonwealth Institute of Entomology.

References.

Barnes, H. F. (1949). Gall midges of economic importance. Vol. VI: Gall midges of miscellaneous crops.—229 pp. London, Crosby Lockwood.

Barnes, H. F. (1956). Gall midges of economic importance. Vol. VII: Gall midges of cereal crops.—261 pp. London, Crosby Lockwood.

Descamps, M. (1956). Insectes nuisibles au riz dans le Nord Cameroun.—*Agron. trop., Nogent* **11** pp. 732–755.

Felt, E. P. (1925). Key to gall midges (a résumé of studies I–VII, Itonididae). —*Bull. N.Y. St. Mus.* no. 257, 239 pp.

Kieffer, J. J. (1913). Diptera. Fam. Cecidomyidae.—*Genera Insect.* fasc. 152, 346 pp.

Rübsaamen, E. H. & Hedicke, H. (1926–39). Die Cecidomyiden (Gallmücken) und ihre Cecidien.—*Zoologica, Stuttgart* **29** Heft 77, 350 pp.

© Commonwealth Agricultural Bureaux, 1959.



FIG. 1. *T. sorghivora*, sp. n.: Pupal cases and exit holes on a stem of *Sorghum vulgare*. (× 3.)



FIG. 2. *T. sorghivora*, sp. n.: Characteristic group of pupal cases above a node on a sorghum stem. (Actual size.)



FIG. 3. *T. sorghivora*, sp. n.: A sorghum stem which has lodged as a result of attack by the midge. (Actual size.)

A NEW GENUS AND TWO NEW SPECIES OF ENCYRTIDAE (HYMENOPTERA, CHALCIDOIDEA) FROM THE BANANA SCAB MOTH, *NACOLEIA OCTASEMA* (MEYR.).

By R. D. Eady

Commonwealth Institute of Entomology.

The material on which this paper is based was bred from *Nacoleia octasema* (Meyr.) in New Guinea. The species of the new genus, herein described, was found to be an important primary parasite of the larva. The *Tyndarichus* species is a hyperparasite.

The new genus is close to *Copidosoma* and *Litomastix*, and very closely resembles the other genera of this group in both structure and habits. In the species described below the male is not unlike the males of some species of *Copidosoma*, and the female resembles *Litomastix*; the species appears to be polyembryonic. In the present state of the systematics of the Encyrtidae it is deemed advisable to describe this species under a new genus.

I am grateful to Dr. J. Ghesquière, who consented to examine material of this genus and was generous in his advice and assistance.

Family Encyrtidae.

Genus **Pseudolitomastix**, gen. n.

Cheeks longer than the height of an eye; mandibles tridentate, the middle tooth slightly longer than the outer teeth (fig. 3); head, mesoscutum and scutellum with shining reticulate sculpture; marginal vein punctiform; antennae with scape normal, slightly flattened; female with the funicle 5-segmented and club obliquely truncate; male with the funicle 6-segmented and club apically acute.

Pseudolitomastix nacoleiae, sp. n.

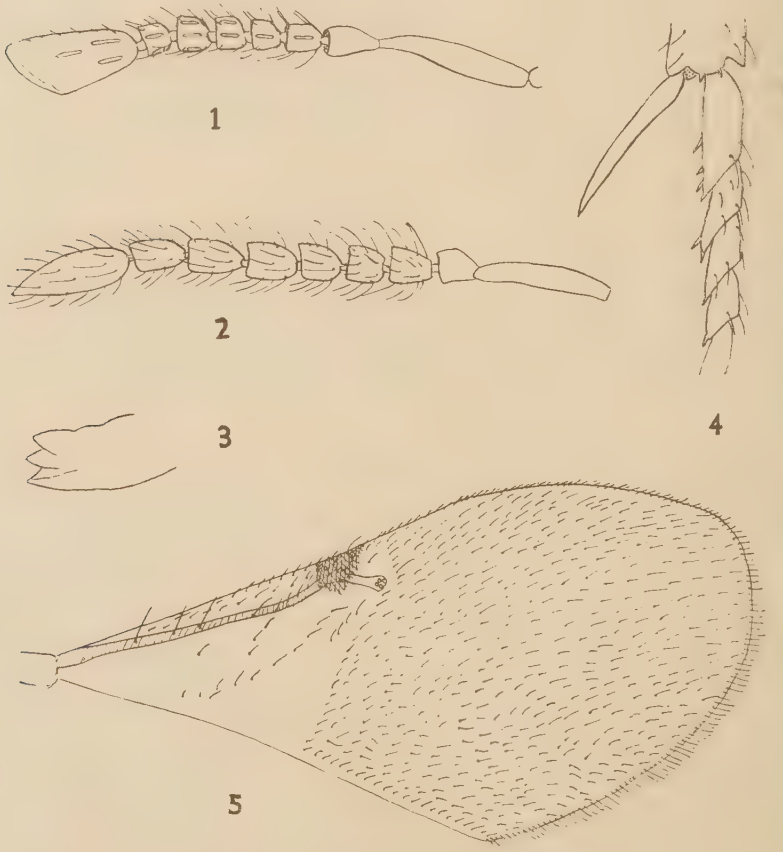
♀. Length 0·7 mm.; head, mesoscutum, mesopleura, and scutellum with shining reticulate sculpture, the scutellum being rather less strongly sculptured. Head and mesoscutum green, the former with purplish reflections; scutellum purple with green apex; mesopleura dark violet; gaster metallic fuscous-green; antennae with scape yellow and flagellum brown; legs with fore femora, middle of femora of second pair of legs, and proximal two-thirds of tibiae of hind legs, and apices of tarsi brown, remainder of legs yellow, tarsi a little paler.

Head with ocelli arranged in a right-angled triangle, the lateral ocellus about two-thirds its greatest width from the margin of the eye; eyes sparsely pubescent; cheeks clearly longer than the height of an eye. Antennae (fig. 1) clavate, with funicle of five segments; scape slightly longer than club, and about equal to four segments of the funicle; pedicel with length about one and a half times width; first segment of funicle clearly longer than broad, remainder quadrate or slightly broader than long; sensilla placodea appear on the funicle segments and the club, but vary both in number and position in different specimens. Mandibles clearly tridentate, the middle tooth being slightly longer than the others (fig. 3). Forewing (fig. 5) without pubescence basally, except for a few larger setae; marginal vein punctiform; postmarginal very short, no longer than marginal, and indistinct; radius a little longer than marginal and postmarginal together, but very indistinct;

marginal, postmarginal, and base of radius covered by a pale fuscous spot. Spur of middle tibia as long as first and second segments of tarsus together (fig. 4); first segment of tarsus slightly shorter than second and third segments together.

♂. Differs from female as follows:— Darker; antennae yellowish brown, filiform (fig. 2); funicle with six segments, at least distal segments a little longer than broad, and all with long hairs which are as long as width of segment or longer; scape longer than club, and about equal to three proximal segments of funicle together; pedicel short, shorter than segments of funicle, and only slightly longer than broad; all femora and hind tibiae brown; fore and middle tibiae tinged with brown in middle.

Material.—New Guinea: Lae, *ex Nacoleia octasema*; iii.1957 (*R. W. Paine*) 9 ♀♀, 7 ♂♂; vi.1957 (*R. W. Paine*) 23 ♀♀, 39 ♂♂. Type ♀, allotype ♂, and 23 paratypes selected from second batch (vi.1957) and deposited in British Museum (Nat. Hist.).



Figs. 1–5.—*Pseudolitomastix nacoleiae*, sp. n.: (1) left antenna of ♀; (2) left antenna of ♂; (3) left mandible of ♀; (4) spur of middle tibia of ♂; (5) right forewing of ♀.

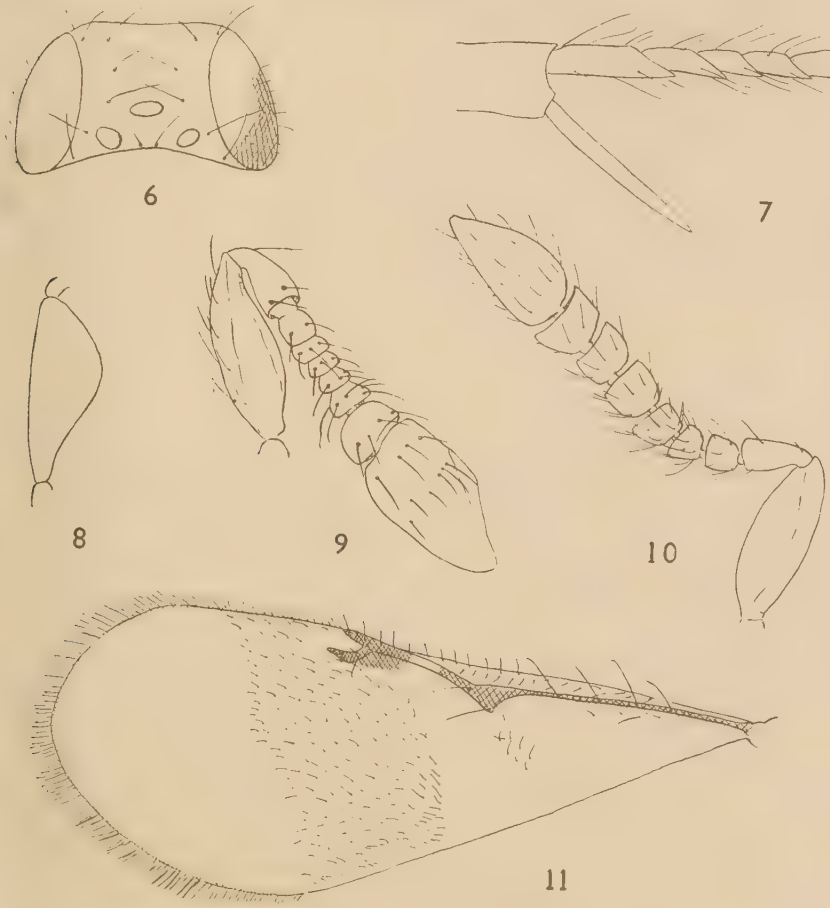
Genus **Tyndarichus** Howard.

Howard, 1910, Tech. Ser. U.S. Bur. Ent. no. 19 (1) p. 5.

Tyndarichus clavatus, sp. n.

♀. Length 0·8 mm. Head, mesoscutum, scutellum and mesopleura with weak reticulate sculpture, and minute punctate microsculpture, and with scattered stout bristles on the vertex of the head (fig. 6), and dorsum of the thorax. Head, dark metallic green; thorax and gaster rather dull metallic black, with greenish and purple reflections; antennae with scape and flagellum dark yellow, and club brown; legs with front and hind femora dark brown, middle femora brown tinged, all tibiae and tarsi dark yellow, and apices of tarsi brown.

Head with face forming a right angle with fronto-vertex; vertex broad, the shortest distance across it, between the eyes, more than twice the width of an eye (fig. 6); ocelli arranged in an obtuse triangle, the longest measurement across



Figs. 6–11.—*Tyndarichus clavatus*, sp. n.: (6) head of ♀, dorsal view; (7) spur of middle tibia of ♀: *Tyndarichus scaurus* Walker; (8) scape of ♀, dextro-lateral view: *T. clavatus*, sp. n.; (9) right antenna of ♀; (10) left antenna of ♂; (11) left forewing of ♀.

a posterior ocellus a little more than the shortest distance between the ocellus and the eye. Eyes with distinct pubescence, long though not dense. Mandibles clearly tridentate. Antennae (fig. 9) strongly clavate, with scape flattened, its length two and half times its greatest width, and a little more than the length of the funicle; the latter with six segments, all transverse; the pedicel half as long as funicle; the club solid and about equal in length to the funicle. Forewing (fig. 11) with subcosta with very distinct triangular expansion apically; marginal with length a little more than four times breadth; postmarginal short, rather more than half radius; radius shorter than marginal; surface of wing, basad of marginal, bare except for a small group of setae below triangular expansion of subcosta, and two or three setae immediately below subcosta between expansion and base of wing. Spur of middle leg as long as first two tarsal segments together (fig. 7). Terebra hardly projecting beyond apex of gaster.

♂. Differs from female as follows: — Antennae (fig. 10) with scape dark yellow and flagellum light brown, less clavate; scape broader and flattened, length twice greatest width, and clearly less than length of funicle; segments of funicle, except first, with lengths varying from a little less than width to very slightly more than width; first segment of funicle always a little longer than broad; club narrower.

Material.—New Guinea: Lae, 41 ♀♀, 12 ♂♂, *ex Pseudolitomastix nacoleiae* on *Nacoleia octasema*, 20.vi.1957 (*R. W. Paine*). Type ♀, allotype ♂, and 24 paratypes in British Museum (Nat. Hist.).

The female of this species can be distinguished from the Palaearctic species of the genus by the completely solid club of the antennae. It is further distinguished from *scaurus* (Wlk.) by the broad vertex, and differently shaped scape (fig. 8); from *rudnevi* Nowicki by its relatively broader scape and very short postmarginal vein; and from *laeviscutellum* Merc. by the sculptured scutellum.

References.

Erdös, J. & Novicky, S. (1955). Genera Encyrtidarum regionis palaearcticae.—*Beitr. Ent.* **5** pp. 165–202.

Ferrière, C. (1953). Encyrtides paléarctiques (Hym. Chalcidoidea). Nouvelle table des genres avec notes et synonymies.—*Mitt. schweiz. ent. Ges.* **26** pp. 1–45.

Girault, A. A. (1915). Australian Hymenoptera Chalcidoidea. VII. The family Encyrtidae with descriptions of new genera and species.—*Mem. Qd Mus.* **4** pp. 1–184.

Mercet, R. G. (1921). Fauna Iberica. Himenópteros, fam. Encírtidos.—732 pp. Madrid, Mus. nac. Cienc. nat.

Nowicki [Novicky], S. (1928). Eine neue Tyndarichus-Art, *T. rudnevi* n. sp., aus den Eiern von Cerambyx cerdo L. (Hym. Chalcidae).—*N. Beitr. syst. Insektenk.* **4** pp. 17–27.

© Commonwealth Agricultural Bureaux, 1959.

OBSERVATIONS ON AN ABNORMAL FORM OF *CALLOSOBRUCHUS MACULATUS* (F.).

By G. H. Caswell

Department of Agriculture, University College, Ibadan, Nigeria.

Callosobruchus maculatus (F.) is an important pest of cowpea (*Vigna unguiculata*) both in the field and in store. It occurs wherever cowpea is grown, and numerous articles have been written on its biology and importance. An extensive bibliography of these is given by El-Sawaf (1956). An abnormal form was reported by Utida (1954) and by Caswell (1956). Southgate, Howe & Brett (1957) give an account of its external features in a general paper on the taxonomy of the group.

The abnormal female is quite distinct from the normal in both external and internal characters, in behaviour and in length of life. The male is distinct only in its internal characters and in its length of life before emergence from the cowpea.* Other features of the abnormal male are less marked and merge into those of the normal form. Utida (*loc. cit.*) calls the abnormal form the " flight " form, since when the female was dropped from a height of 30–50 cm. it flew to the side of a container, while the normal form fell to the bottom. Southgate, Howe & Brett (*loc. cit.*) call the abnormal form the " active " one, and this is considered a better description since the normal female is capable of flight and the abnormal male does not show the flight characteristic mentioned by Utida. For these reasons the abnormal form will be called the " active " form in this paper.

Characters of the two Forms.

External characters.

Plates showing the normal and active forms are given by Southgate, Howe & Brett (*loc. cit.*), who describe the patterns found on the elytra in both sexes of the normal and active forms. They say that the ground colour of the elytra in the active form of the female is " almost wholly black." It has been observed in these experiments that the colour of the elytra for both normal and active forms varies from completely testaceous to almost completely black; and in both forms is most commonly testaceous with well-defined black areas, as shown in fig. 1.

In such individuals the black areas are devoid of pubescence in both normal and active forms. The distribution of pubescence on the elytra remains fairly constant in spite of variation of elytral colour; thus, although the black areas may be larger or smaller, the area of bare cuticle will remain constant. The difference in elytral colour between the normal and active forms lies in the pubescence. In the active form, the elytra, except for those areas already mentioned, are thickly covered with golden and white pubescence, making the dull black areas of bare cuticle stand out sharply. In the normal form the pubescence is much reduced so that the effect is to make the elytral pattern less definite. The pygidium in the female carries the character that most clearly distinguishes the two forms. In both forms the ground colour is very dark brown to black, and a narrow white stripe of pubescence is present along the centre line.

* The term " emergence " refers throughout this paper to emergence of the adult insect from the cowpea.

In the normal form the rest of the pygidium is bare, but in the active form the rest of the pygidium is covered with dense pale golden pubescence, so that on superficial observation the pygidium of the active form appears to be entirely white, while the normal form has a black pygidium with a narrow white median stripe.

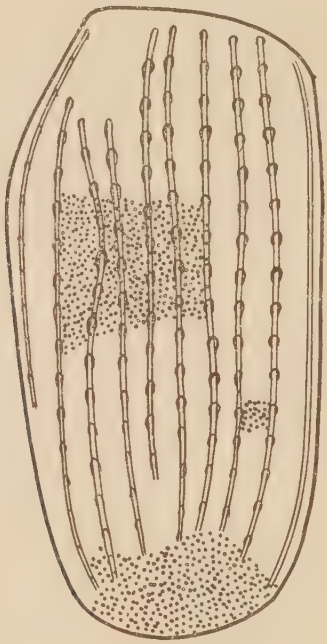


Fig. 1.—Left elytron of a female of *Callosobruchus maculatus*. The commonest distribution of black pigment is shown by the dotted areas.

Internal characters.

The normal male on emergence has a well-developed internal reproductive system consisting of two pairs of testes and four pairs of accessory glands; in the newly emerged active form the internal reproductive organs are undeveloped.

The normal female on emergence has a pair of well-developed ovaries each consisting of six ovarioles each about 1·25 mm. long. The lowest eggs in the ovarioles are approaching maturity and the first eggs are shed into the calyces within a few hours of emergence of the insect from the pea. Fifty-two specimens of the active form were dissected after periods varying from 2 to 92 days after emergence from the pea. The ovarioles were initially rudimentary, being only 0·2 mm. long, and they remained at this size for the first week after emergence. In the second week there was some development of the ovarioles, which reached 0·4–0·6 mm. in length. In two cases out of 11 dissected in the second week, a few eggs had been shed into the calyces; in all cases there was abundant food reserve in the form of discrete fat-body and globules of oil. During the next two weeks the state of the ovarioles remained unchanged unless eggs had been shed into the calyces. In eight out of 19 specimens dissected there were eggs in the calyces; these eggs were never numerous, the average number being seven. It

was clear that this production of eggs had exhausted the food reserves of the insect because in three of the cases where eggs were present it was not possible to find ovarioles, and in only two cases where eggs were present was there any food reserve remaining. In the remaining 20 specimens dissected, after periods from emergence of 29 to 92 days, only four had eggs in the calyces, and the amount of food reserve present showed a steady decline in quantity, until for periods of more than 52 days none was found.

It would seem from these observations that in all cases the internal reproductive system of the active female is rudimentary on emergence and develops slowly during the first two weeks. It never reaches the size of that of the normal female, but after two weeks some specimens produce a few mature eggs, which are shed into the calyces. This process appears to exhaust the food reserves and these individuals probably die. The remainder mature no eggs and food reserves are devoted entirely to prolongation of life.

The following account describes experiments carried out with the Bruchid in southern Nigeria, together with extracts from records kept for a period of five years.

Method.

The experiments were carried out at University College, Ibadan.

Some cowpea is grown locally but most is brought from farther north. There is one cowpea harvest in the year, which takes place in November and December, so that the food supplied to the cultures was fresh at the beginning of each year and became progressively older as the year advanced. Supplies of cowpea were obtained at weekly intervals from the local market, undamaged seeds were selected and the moisture content determined. These selected seeds were then used as food supply for the cultures for the next week. The cultures, originally derived from a wild stock, each consisted of a pair of beetles and single infested cowpeas obtained daily from them. Each day a male and a female were chosen at random from those that had emerged in the cultures since the previous day. These two were placed in a container with ten of the selected cowpeas. On succeeding days the cowpeas were examined, eggs counted and the seeds bearing eggs were placed singly in specimen tubes. Those seeds removed were replaced by the same number of selected seeds. The adults which emerged from the seeds bearing eggs were available for setting up a new culture as described above. Records were kept of the number of eggs laid on each pea, the date of emergence and date of death of the parents, the date of emergence and the sex of the resulting adults, and the form to which the females belonged. Temperature and humidity were recorded daily in the laboratory where the cultures were kept. For purposes of dating a particular culture the date of oviposition is used throughout the paper.

Seasonal Occurrence of the Active Form.

Records of the occurrence of the active form of the female have been kept for three years, and the data, summarised on a monthly basis, are presented in fig. 2.

Each year there is a high incidence of the active form during the months of April and May. This corresponds with the onset of the wet season. At this time the moisture content of the cowpeas is starting to increase, and the air temperature is falling.

Utida (*loc. cit.*) makes no mention of any seasonal occurrence of the active form, and his experiments, designed to test the effect of variations in temperature, humidity, and population density, were not conclusive. He found evidence to show that there might be an association with high moisture content in the cowpeas

in which development had occurred, due to high atmospheric humidity or high population density. In the present series of experiments it was found that moisture content is highest in October, when it is over 15 per cent. At this time there is a low incidence of the active form. In April and May, when the incidence is highest, the moisture content is 12 to 13 per cent.

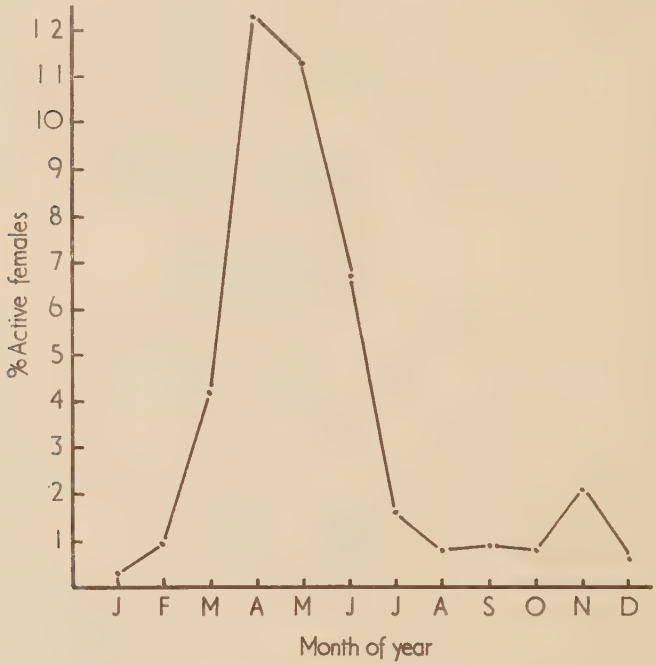


Fig. 2.—Seasonal occurrence of the active form of the female of *Callosobruchus maculatus*.

When seasonal changes in temperature are considered, it is found that the highest temperatures occur in February and March, just before the onset of the rains, and again before the peak incidence of the active form. In the cooler part of the year, the temperatures at which the cultures were kept was raised artificially so as to approximate to that obtaining in February and March, but no increase in the percentage of the active form occurred. So far it has not been possible to rear the Bruchids under constant conditions in order to discover if there is any inherent cyclical factor involved.

In order to investigate the possibility that population density is a factor governing the occurrence of the active form, data were taken from the records for the form of female emerging from cowpeas bearing different numbers of eggs. The data summarised below (Table I) were taken from records for March, April and May 1958, when the active form was most common.

Analysis of variance of these data showed that the number of eggs per cowpea had no significant effect at the 5 per cent. level on the proportion of active females emerging.

The problem is further complicated when the percentage of active females produced in the same culture in succeeding years is considered. The mean percentages of the active form of the female in the months of highest incidence in successive years are shown in Table II.

TABLE I.

The effect of larval density on the incidence of the active form.

No. of eggs per pea	No. of females emerging	
	Normal form	Active form
1	109	26
2	144	45
3	92	37
4	68	17
5	31	13
6	6	3
7	2	—
8	5	3

Rearing from the original stock was continuous throughout the period of observations, and no additional Bruchids were introduced. Records were incomplete in 1954 but the same culture was maintained. With the lapse of time the proportion of the active form decreased, a fact which suggests that in laboratory culture the ability to produce the active form of the female tends to be lost. This was confirmed in 1958 by starting a second series of cultures under identical conditions but using Bruchids taken from an infested store instead of from the

TABLE II.

Percentage of active females produced in the months March–June in successive years.

Year	Mean percentage active females for period March–June
1953	28·7
1954	Records incomplete
1955	17·2
1956	4·7
1957	4·1
1958	4·2

existing cultures. These parallel cultures gave a mean percentage of 18·2 active females for the four months in question. This suggests that continuous breeding in culture involves a selection which tends to eliminate the ability to produce the active form. Utida (*loc. cit.*) concludes from his results that a hereditary factor is not involved, but the above observations might imply that there is such a factor.

To investigate this point further, males and females from the old and new cultures were crossed. Data obtained in this way were compared with those obtained from the two separate series of cultures over the same period. These data for the months of April and May are summarised in Table III.

TABLE III.

Percentage of active females produced by crossing males and females from new and old cultures.

Origin of parents	Percentage active females produced
New male × new female	29·2
New male × old female	15·7
Old male × new female	17·9
Old male × old female	4·5

It would appear from these data that some genetic factor is involved.

Duration of pre-adult Stages.

The time taken for the active form of the female to pass from egg to emergence from the cowpea is longer than it is for the normal form. This was suggested by Utida who had insufficient data to confirm it. The data for the four relevant months of 1955 are summarised in Table IV.

TABLE IV.

Developmental period of normal and active forms of female from egg to emergence.

	Mean time in days ± S.E.		Difference ± S.E.
	Normal form	Active form	
March	25 ± 0·12	32 ± 0·40	7 ± 0·44
April	26 ± 0·14	33 ± 0·23	7 ± 0·27
May	27 ± 0·13	35 ± 0·31	8 ± 0·33
June	30 ± 0·17	36 ± 0·39	6 ± 0·42

It is evident that the time taken by the active form is significantly longer than that taken by the normal form of the female. The data available for the active form of the male indicates that the time taken to pass from egg to emergence from the cowpea is similar to that taken by the active female.

In an attempt to investigate this delay, undamaged cowpeas were kept at a constant humidity and weighed periodically until their individual weights remained constant on two successive weighings. Females were allowed to oviposit on these peas and all the eggs were removed except one per pea. Each pea was weighed daily from the first day after egg-laying until the adult derived from the egg emerged. Two typical graphs (fig. 3) show the change in weight of two peas, one which contained a developing normal female and the other a developing active female.

The development of *C. maculatus* has been given by Larson & Fisher (1938) and may be summarised as follows: The incubation period of the egg is three or four days. The first-instar larva is specially adapted for boring, whereas subsequent larval instars are adapted for feeding. After emerging from the pupa the adult spends a few days within the pea before making its way out.

The activity of the feeding larval stages is clearly reflected in the rapid fall in weight of the pea (fig. 3). After this fall the weight remains approximately constant during the non-feeding, pupal and adult stages. It is evident that it is this last period which is prolonged in the active form of the female. The final drop in weight results from emergence of the adult from the seed.

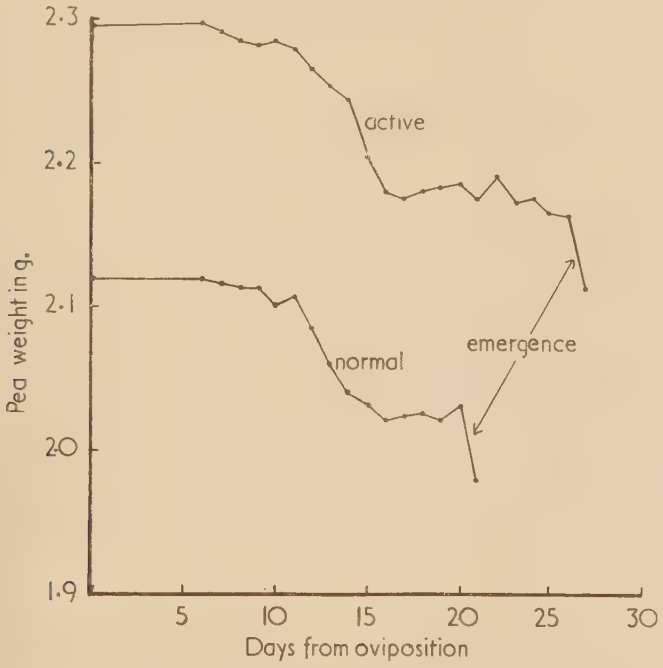


Fig. 3.—Change in weight of cowpeas infested with a larva of *Callosobruchus maculatus*.

Duration of Adult Life.

Newly emerged normal and active females were kept in isolation until death and the length of life was recorded. Similar records were obtained for normal and active females which were placed with males. Results are summarised in Table V.

On emergence, the amount of food reserves carried by normal and active females appears to be about the same. The normal female immediately produces eggs and as many as 30 may be found stored in the calyces of unmated females. Some of these may be laid although the female does not mate, but it seems unlikely that their reserves of nutrients can be withdrawn for use by the parent. The active female, on the other hand, frequently produces few, if any, eggs. It follows that the active female will have food reserves to prolong life

which in the normal form are used to mature eggs. The normal female has been found to lay an average of 67 eggs, yet dissection never revealed more than 30 stored in the calyces of unmated females. These females had not laid any eggs, and it is presumed that the pressure produced within the calyces had inhibited the maturation of more eggs. This being so, there is surplus food material available in unmated normal females which would have been used to produce the additional eggs and is now available to prolong life.

TABLE V.

Mean length of life in days of mated and unmated females ± S.E.

Normal		Active	
Mated	Unmated	Mated	Unmated
6 ± 0·3	11 ± 0·3	13 ± 1·0	33 ± 0·3

No certain explanation can be offered for the considerable reduction in length of life of active females when these are confined with males. In a few cases eggs were laid, but there was no significant difference between the length of life of those active females which produced eggs and those which did not. It has, however, been observed that in the absence of a male the active female will usually rest on the lid of the container, whereas when a male is present the female will usually be moving to avoid the attention of the male. It seems possible that it is this constant movement on the part of the female which uses up food reserves and so reduces the length of life. Some doubt is cast on this possibility by the fact that when normal females are confined with males for only a limited period there is no significant change in either egg production or in length of life of the female as compared with one confined with a male continually.

Oviposition.

It has already been shown that the reproductive system of the active female does not mature until a week or more after emergence. For this reason it was thought possible that the time when a male was placed with an active female might have some bearing on the number and fertility of eggs produced. Males were therefore placed with active females for one day only immediately on emergence, continuously throughout the life of the female starting from the day of its emergence, or continuously throughout the remainder of the life of the female, starting one week and two weeks, respectively, from its emergence. The results are summarised in Table VI.

There is insufficient data for analysis, but it is clear that, under the conditions tested, between a quarter and a half of the active females will produce a few eggs. It will be recalled that when active females were dissected at various times after emergence, 14 out of 52 specimens were found to have eggs in the calyces. This agrees closely with the results given in Table VI. It would seem, therefore, that the presence of a male does not stimulate the production of eggs but may cause eggs to be laid which might otherwise be retained within the calyces.

Out of the 28 pairs producing eggs, four pairs produced some which were

fertile. Three of these were from pairs which were mated continuously from the time of emergence of the female and one from those mated two weeks after the emergence of the female. Apparently normal males and females were produced in each case.

TABLE VI.

Egg-production by active females.

Nature of experiment	No. of trials	No. of females producing eggs	Total no. of eggs
Mating for 1 day only	8	2	4
Continuous mating from emergence..	52	11	84
Continuous mating after one week ..	20	11	95
Continuous mating after two weeks..	13	4	15

Summary.

Under certain conditions, *Callosobruchus maculatus* (F.) produces males and females which are distinct from the normal ones. These are called here the "active" form, and in southern Nigeria they occur most commonly during the months March to June. The active form has a longer pre-adult stage than has the normal form and it flies readily, unlike the normal form. There is some evidence which indicates that a genetic factor is involved in the production of the active form but no clear indication as to what external factors are involved. The normal female has mature eggs in its calyces within a day of emergence, and will lay about 60 eggs. The active female was found to have immature ovaries on emergence and these did not develop to any great extent in the conditions employed. About three-quarters of the active females never produce any eggs, and the rest produce an average of seven. This difference in egg-production probably makes food reserves available which are used to prolong the life of the active female. The eggs laid by active females are rarely fertile, and when adults do emerge they are apparently normal males and females.

Acknowledgements.

I am particularly indebted to Rev. M. F. Wiles of the Department of Religious Studies, University College, Ibadan, for a translation of the paper by Prof. S. Utida.

References.

Caswell, G. H. (1956). Observations on the biology of *Callosobruchus maculatus* F. (Coleoptera: Bruchidae).—*Divl. Rep. Fac. Agric. Univ. Coll. Ibadan* (Ent.) no. 3, 9 pp., multigraph.

El-Sawaf, S. K. (1956). Some factors affecting the longevity, oviposition, and rate of development in the southern cowpea weevil, *Callosobruchus maculatus* F. (Coleoptera: Bruchidae).—*Bull. Soc. ent. Egypte* **40** pp. 29–95.

Larson, A. O. & Fisher, C. K. (1938). The bean weevil and the southern cowpea weevil in California.—*Tech. Bull. U.S. Dep. Agric.* no. 593, 70 pp.

Southgate, B. J., Howe, R. W. & Brett, G. A. (1957). The specific status of *Callosobruchus maculatus* (F.) and *Callosobruchus analis* (F.).—*Bull. ent. Res.* **48** pp. 79–89.

Utida, S. (1954). " Phase " dimorphism observed in the laboratory population of the cowpea weevil, *Callosobruchus quadrimaculatus*. [*In Japanese with English summary.*]—*Oyo-Dobuts. Zasshi* **18** pp. 161–168.

© Commonwealth Agricultural Bureaux, 1959.

THE BREEDING BEHAVIOUR OF THE TYPE FORM OF *AËDES* (*STEGOMYIA*) *AEGYPTI* (L.) IN SOUTH-WESTERN NIGERIA IN RELATION TO INSECTICIDAL CONTROL.

By Gordon Surtees *

In the second report of the Expert Committee on Yellow Fever of the World Health Organization (1948) it was stated, that in view of the lack of data concerning the ecology of *Aëdes* (*Stegomyia*) *aegypti* (L.) in Africa and the problems involved in its eradication, an experiment should be aimed at the eradication of the species in a selected area where it was known to be responsible for man to man transmission of yellow fever. With this recommendation in mind, ecological studies have been conducted by the writer in southern Nigeria with particular emphasis on the breeding behaviour of the species and the aim of this paper is to bring these results to bear upon the problem of control of *A. aegypti* in this part of Africa.

South-western Nigeria may be divided into three zones, namely, the coastal mangrove swamp, the freshwater swamp which extends up to 10 miles inland, and the rain-forest which at some points is found as far as 150 miles from the coast. One of the most widespread species encountered was *A. aegypti* which was represented in all cases by the type form (Mattingly, 1957). In the mangrove swamp it was found breeding in the basins of rotting tree stumps, in the freshwater swamp zone and in the region of Lagos it bred in holes in growing trees whilst in the rain-forest it was totally domestic being restricted to domestic-container habitats in the immediate vicinity of village clearings. Thus, due to this changing pattern of behaviour, associated with other aspects of its biology which will be discussed here, *A. aegypti* presents diverse problems from the point of view of control.

Survey Methods.

Apart from general surveys of the three zones already noted, which were qualitative in nature, two quantitative surveys were carried out to study the breeding behaviour of *A. aegypti*. The first was in the rain-forest zone some 50 miles north-west of Lagos in the Yoruba village of Ilobi (6°45′N. 3°5′E.) a detailed account of which will be found elsewhere (Surtees, 1959*a*). During qualitative studies in and around the village it was evident that there was negligible breeding in natural habitats such as tree holes beyond the village boundary. Over 90 per cent. of all larvae found were in domestic containers within the village and it was noted that pots which were in any way contaminated with decaying vegetable matter did not contain larvae. This behaviour pattern was studied in detail as follows. Baked clay pots holding about half a gallon of water were used and placed out in three groups, inside houses, outside but in otherwise sheltered positions and in fully exposed positions where the water was subject to heating by the sun. These were examined weekly. Larvae found in any pot were transferred to 3 × 1 glass tubes for future identification and the number of pots in each situation infested with larvae recorded. After each inspection the pots were scoured out and refilled with fresh water.

* Formerly Entomologist, West African Council for Medical Research, Lagos, Nigeria. Now at Pest Infestation Laboratory, London Road, Slough, Bucks.

The second survey was carried out in Lagos, the main part of which is situated on an island some 2½ miles long from east to west and a mile across at its widest point. It is bordered on the south and west by the deep-water harbour, on the north by the inland Lagoon and on the east by an adjacent island. The Island is intersected by a modern system of major and minor roads and there is running water in all of the main streets either in the actual buildings or in the form of street hydrants. This obviates the need for water storage which is a common feature of the villages. Whilst tree-hole breeding of *A. aegypti* was known in this area, a pot survey was carried out to investigate any domestic behaviour and to obtain some indication of its relative abundance. Accordingly, pots were placed out in a similar manner to the Ilobi survey and the same routine followed.

Results of Surveys.

The results of these two surveys are given in Table I. In the Ilobi survey there was marked domesticity on the part of the breeding mosquito, pots which were exposed being largely avoided, whereas in the Lagos survey a less domestic breeding pattern was discernible, there being relatively less breeding inside houses. Furthermore, in the village, larvae were noticeably absent from pots containing any decaying vegetable matter whilst larvae were commonly found in such pots in Lagos.

TABLE I.

The degrees of pot infestation by larvae of *Aëdes aegypti* in the village and Lagos surveys.

Position of pots	Pot infestation					
	ILOBI			LAGOS		
	No. examined	No. infested	(%)	No. examined	No. infested	(%)
Inside houses ..	90	49	54·3	120	48	40·0
Outside (sheltered) ..	90	28	31·3	437	151	34·6
Outside (exposed) ..	120	17	14·1	439	104	23·7
Total	300	94	31·4	996	303	30·5

Spraying Tests.

During the latter part of 1957, spraying tests were carried out in Ilobi village to ascertain the relative efficiency of two insecticidal control methods against *A. aegypti*. In the first test, DDT was sprayed from an Auster B.8 aircraft using Micronair rotary atomisers. The insecticide was a 5 per cent. solution in gas oil which was distributed at the rate of 0·5 lb. per acre. The droplet size was 80 microns. The aircraft flew at 30–40 ft., and a 20- to 30-ft. swathe was laid down. In the second test, dieldrin was used in a 15 per cent. solution in oil. This was distributed by means of a swingfog apparatus, using a nozzle size of 0·8 mm., which gave an approximate rate of distribution of 0·8 oz. per acre. During both tests, fourth-instar larvae of *A. aegypti* were exposed in clay pots in a variety of situations, including inside and immediately outside houses under overhanging eaves, in ground flora within the village and beneath bush and tree canopy on the village edge. Twenty-four hours after each spray the number of dead larvae was recorded. Larvae in covered pots were used as controls.

The results of the aerial spraying are given in Table II and are grouped according to the positions of the pots. The control larvae suffered no mortality. In the ground fogging test, larvae within the houses suffered mortalities of from 80 to 100 per cent., and those in vegetation 50 to 80 per cent. Adults exposed in cages within houses all died but eggs exposed in petri dishes were not affected. The higher mortalities within houses in the second test were due to the fact that

TABLE II.

Grouped mortality results of fourth-instar larvae of *A. aegypti* 24 hours after aerial application of DDT.

Positions of pots	No. larvae exposed	Mortality after 24 hours	
		No.	%
Inside houses	200	4	2·00
Immediately outside	200	3	1·50
In ground flora	200	167	83·50
Beneath bush and tree canopy ..	160	80	50·00
Total	760	254	33·40

the actual rooms containing the mosquito larvae were sprayed. One week after the second test, the density of pot infestation had fallen to 17 per cent. inside houses and 7·7 and 9·9 per cent., respectively, in the sheltered and exposed situations. Three weeks after the spray, a pot survey showed that the mosquitos had returned to a density equal to that found before the first application.

Discussion and Conclusion.

Aëdes aegypti, in the studies described here, was represented throughout by the type form of the species. Past workers in West Africa generally agreed in their findings that this species was typically domestic in its breeding habits although breeding has also been recorded from tree holes (Dalziel, 1920; Dunn, 1928; Kumm, 1931). Mattingly (1952) concluded that the only species of the subgenus *Stegomyia* regularly found in small containers in, or immediately about houses, was *A. aegypti*, and Strode (1951) pointed out the epidemiological importance of such a close association with man.

The studies in Ilobi emphasised the domestic nature of the mosquito in that breeding was restricted to domestic containers within the immediate vicinity of the village, whilst in Lagos a less domestic pattern on the part of the ovipositing female had to be accounted for. The lack of water storage within Lagos serves to restrict domestic breeding, and it may be suggested, therefore, that the population there, which breeds typically in tree-holes possesses a latent or suppressed domestic behaviour pattern. For the Ilobi strain it was shown that vegetable contamination of water restricts the egg-laying behaviour of the female (Surtees, 1960) so that larvae were only found in clean water, whereas the Lagos population was commonly found in contaminated water, suggesting a greater tolerance on the part of what is now a tree-hole breeding population to this feature of the environment. The tree-hole breeding habit may indicate a reversion in behaviour on the part of this mosquito. Morphological evidence (Surtees, 1959*b*) indicates that the tree-hole habitat was the original one for this species, and during the course of its evolution it has become adapted to the domestic environment so that any tree-hole breeding would represent a reversion to the more primitive habit. In the region of Lagos, therefore, although the

species could at one time have bred in water pots in the town, the population now breeds in scattered tree holes on the Island perimeter and on the adjacent one to the east, the domestic pattern of behaviour being masked, only becoming evident when container habitats are presented.

Measures against *A. aegypti* are made more difficult by the fact that the majority of immature forms are localised in relatively inaccessible habitats such as tree holes or water containers inside houses. The original objective of the present work was to investigate the possibility of eradicating the species in a selected area. The results obtained suggest that eradication, or total elimination of the species, is unattainable over any wide area due to the plasticity of its breeding behaviour and to the purely mechanical difficulty involved in locating and treating all available breeding sites. On the other hand, control measures that would reduce the numbers of the species and maintain them at a low level would be feasible. Carter (1931) pointed out that as the mosquito density is lowered by anti-larval measures, the numbers of adults becomes too small for the virus to be maintained; at the same time transmission from man to man is interfered with so that the disease gradually dies out in the controlled area.

In both of the spraying tests described here it was evident that the shelter provided by houses and foliage afforded a high degree of protection to the immature forms of the mosquito, but in the ground fogging test, where the interiors of houses were sprayed, high mortalities were obtained. Since there was negligible breeding in the natural habitats in the forest, no information is available on the effectiveness of the treatments against a non-domestic population of the mosquito. But to deal with such a population a high degree of penetration is essential if the larvae and adults are to be reached. Slow-flying aircraft would be expected to facilitate this, due to the downward displacement of air and the strong wing-tip vortices, whilst helicopters would be an even more efficient method to ensure foliage penetration. A further factor concerned in penetration is droplet size, the smaller the droplet the greater the chance of filtering through the upper canopy and reaching the lower storeys.

In the opinion of the present writer the most efficient method of control against domestic and non-domestic populations of the mosquito is one which ensures treatment of individual larval habitats. This could be done by the use of insecticidal pellets. The use of these against domestic mosquitos has been discussed by Elliott (1955) where the pellets in question were made up of 3 parts plaster of paris to 1 part BHC wettable powder containing 6·5 per cent. of γ isomer. When placed in larval habitats, these produced 100 per cent. mortalities for periods up to 134 days. Whilst such a method could not be tested at the time by the writer, it should perhaps be pointed out that the hazard to man of such applications to water which may be consumed is not great. In a Clinical Memorandum on Economic Poisons (1956) the United States Department of Health Education stated that an acute dose for man of γ BHC is in the region of 7–15 g., whilst they point out that with regard to a chronic dose it has been found that BHC is rapidly excreted by laboratory animals so that there is no accumulation within the body.

Some mention should also be made of the time of year when such a control project may best be carried out. It is suggested that, for this particular area, the commencement of the rains (March–April) would be most suitable. At this time the eggs which would have remained viable over the dry season would begin to hatch out, for it has been found in this species that the eggs laid at the end of one wet season (November–December) provide the initial population at the onset of the next rains (Surtees, 1958*a*). Thus pellets placed in potential sites at the time of, or before the first showers would ensure that the initial population of larvae would be killed and those mosquitos reaching the adult stage from any untreated sites would only have treated sites in which to oviposit.

A further difficulty involved in the control of the species is that it rapidly develops resistance to an insecticide such as DDT (R. Elliott, personal communication; Surtees, 1958*b*) and naturally occurring resistant populations are known, the latter problem being recently reviewed by Brown (1958). Checks upon such an eventuality that should be maintained are, estimating the initial tolerance to the insecticide in use, a study of the possible development of resistance under laboratory conditions, and frequent field observations. Finally the possibility must not be overlooked of the establishment of wild populations in forested areas when a campaign is directed against a domestic mosquito. This may be caused by the development of behaviouristic resistance (Brown, 1958) in which case the oviposition behaviour of the female may be altered, or by naturally occurring tree-hole breeders building up in numbers and becoming the dominant population in the area. Both possibilities must be considered in view of the marked plasticity in breeding behaviour of this species.

Summary.

The type form of *Aëdes* (*Stegomyia*) *aegypti* (L.) is widespread in south-western Nigeria, breeding in the basins of rotting tree stumps in the coastal mangrove swamp, in holes in living trees in the freshwater swamp zone and near Lagos and in domestic containers restricted to village clearings in the inland forest zone. Pot surveys were carried out in a rain forest village 50 miles north-west of Lagos and in the capital itself. Baked clay pots holding half a gallon of water were used in each case and were placed in three situations, inside houses, outside but in otherwise sheltered positions, and in fully exposed positions. The degree of larval infestation in both cases was greatest inside houses, but the behaviour pattern was less domestic in Lagos. Larvae were found in pots contaminated with decaying vegetable matter in Lagos but not in the village. Spraying tests indicated that houses and foliage afforded varying degrees of protection to the immature stages of the mosquito. Control of this species is made difficult by the localisation of the immature stages in relatively inaccessible sites and it is suggested that individual treatment of larval habitats by insecticidal pellets before the commencement of the rainy season would ensure a high mortality of first-generation larvae. The toxicity hazard to man is not considered to be great. The development of resistant and wild populations is discussed.

References.

Brown, A. W. A. (1958). Insecticide resistance in arthropods.—*Monogr. Ser. World Hlth Org.* no. 38, 240 pp.

Carter, H. R. (1931). Yellow fever. An epidemiological and historical study of its place of origin.—308 pp. Baltimore, Md., Williams & Wilkins.

Dalziel, J. M. (1920). Crab-holes, trees, and other mosquito sources in Lagos. —*Bull. ent. Res.* **11** pp. 247–270.

Dunn, L. H. (1928). Further observations on mosquito breeding in tree-holes and crab-holes.—*Bull. ent. Res.* **18** pp. 247–250.

Elliott, R. (1955). Larvicidal control of peridomestic mosquitoes.—*Trans. R. Soc. trop. Med. Hyg.* **49** pp. 528–542.

Kumm, H. W. (1931). Studies on *Aëdes* larvae in south-western Nigeria and in the vicinity of Kano.—*Bull. ent. Res.* **22** pp. 65–74.

Mattingly, P. F. (1952). The sub-genus *Stegomyia* (Diptera, Culicidae) in the Ethiopian Region. I.—*Bull. Brit. Mus.* (*nat. Hist.*) Ent. **2** pp. 235–304.

Mattingly, P. F. (1957). Genetical aspects of the *Aëdes aegypti* problem. I. Taxonomy and bionomics.—*Ann. trop. Med. Parasit.* **51** pp. 392–408.

Strode, G. K. *Ed.* (1951). Yellow fever.—710 pp. New York, McGraw Hill.

Surtees, G. (1958*a*). Laboratory studies on the survival of the eggs of *Aëdes* (*Stegomyia*) *aegypti* under adverse conditions.—*W. Afr. med. J.* (N.S.) **7** pp. 52–53.

Surtees, G. (1958*b*). The production of DDT resistance in a Southern Nigerian strain of *Aëdes* (*Stegomyia*) *aegypti* under laboratory conditions.—*W. Afr. med. J.* **7** pp. 114–116.

Surtees, G. (1959*a*). On the distribution and seasonal incidence of Culicine mosquitoes in Southern Nigeria.—*Proc. R. ent. Soc. Lond.* (A) **34** pp. 110–120.

Surtees, G. (1959*b*). Functional and morphological adaptations of the larval mouthparts in the sub-family Culicinae (Diptera) with a review of some related studies by Montschadsky.—*Proc. R. ent. Soc. Lond.* (A) **34** pp. 7–16.

Surtees, G. (1960). Studies on the breeding behaviour of *Aëdes* (*Stegomyia*) *aegypti* L. in Southern Nigeria.—*Ent. mon. Mag.* **96** (*in press*).

World Health Organization (1948). Second report of the Expert Committee on Yellow Fever. Geneva.

© Commonwealth Agricultural Bureaux, 1959.

OBSERVATIONS ON THE MOSQUITO, *AËDES* (*STEGOMYIA*) *AEGYPTI* (L.), IN EAST AFRICA.

II.—THE BITING CYCLE IN A DOMESTIC POPULATION ON THE KENYA COAST.

By G. A. H. McClelland *

East African Virus Research Institute, Entebbe, Uganda.

In the first paper of this series (McClelland, 1959) it was shown that, in an outdoor population of *Aëdes aegypti* (L.) from Entebbe, Uganda, there was a sharply defined diel † rhythm of biting and general activity which was very like the laboratory oviposition cycle found by Haddow & Gillett (1957). This biting cycle was similar to the cycles found in other outdoor populations of *A. aegypti* (Teesdale, 1955; van Someren, Heisch & Furlong, 1958), but different from the rather ill-defined cycles found by these workers and Lumsden (1957) in indoor and peridomestic populations. Differences between the cycles in various sites have also recently been demonstrated by Boorman (1958) in a village in Nigeria.

Mattingly (1957) gives criteria for separating, on morphological grounds, three forms of *A. aegypti*, which show different habitat preferences. In all the above studies where more than one form was taken, no quantitative differentiation was made. The possible effects of differences in environment are thus complicated by those of differences in population composition.

Before any conclusions on the biting cycle of *A. aegypti* could be reached, further series of 24-hour catches, with separation of the three forms of *A. aegypti*, in a locality where they are found together, were necessary. The present paper presents the results of 20 such catches.

Locality.

The locality chosen was the village of Ganda, five kilometres inland from Malindi on the Kenya coast, at an altitude of less than 50 metres above sea-level. It is situated in the fertile belt running between the poor coastal coral soil and the arid hinterland; the predominant cover is extensive coconut plantations interspersed with mango, cashew-nut and kapok trees. Cultivated patches of banana, maize and cassava, secondary bush and grass, occur in open areas and under the light shade of the palms. Mosquito breeding sites are varied and numerous. Rot holes and crotch holes in the trees and step holes in the palms are abundant. Coconut shells, banana-flower bracts and, near the houses, old tins and other litter form a variety of breeding sites on the ground, and breeding in plant axils is common. Within the village, rain-water barrels are common and some water is customarily stored within the houses. A fuller description is given by van Someren, Heisch & Furlong (1958).

The better houses are well constructed of poles, coral stone and mud, and are usually joined by palm-leaf fences to a smaller, servant's hut at the back so as to form an enclosed compound. The first ten catches took place in such a compound about three metres wide by four metres long; the eaves of the two houses projected so that about half the area was under shelter. The second ten cathes

* Now at Department of Entomology, London School of Hygiene and Tropical Medicine.

† For definition of 'diel' see Haddow & Gillett (1957, p. 164).

took place within a room opening narrowly, without a door, on to the same compound. These catching sites correspond very closely to those used by van Someren, Heisch & Furlong (1958) in the same village.

In the year of the catches, the rains were about a month later than usual. Sufficient rain to promote outside breeding did not occur until 20th May, and the many temporary lakes, which have usually formed by the end of April, did not appear until after heavy rainfall on 2nd and 3rd June. Winds were moderate throughout the period.

Methods.

As before, the method is based on the 24-hour catch devised by Haddow (1945, 1954). The first series of ten catches, beginning on 21st April 1958 and continuing at three-day intervals, was carried out in the hut compound during the dry period. The second series of ten catches, beginning on 26th May and continuing at the rate of two per week, was carried out inside the hut during the wetter period. During the first series the inhabitants of the house went about their normal routine, but in the interior series the members of the catching team were the only occupants of the room.

The catching team of five locally recruited men received initial training in several single-hour test catches. Three men worked and two rested, one man changing in rotation every hour. Catching began at 1700 hr. 'catch time' (Lumsden, 1952), the first hour's catch being discarded so that the effective 24-hour period ran from 1800 hr., which was the exact time of sunset. During the night, the catchers worked by the light of a single hurricane lamp. The author personally supervised the catches from the start until shortly after sunrise, when his place was taken by an African supervisor with previous experience of ten 24-hour catches. The author returned during the last hour of each catch, when the accuracy of the clock was checked. Thus the least possible responsibility was given to junior staff. In other respects the methods follow the description in the first paper.

Before the author's arrival, aluminium pots had been placed in a number of houses at Ganda through the kind co-operation of the Kenya Medical Department; a headman's house, which on inspection showed the highest incidence of larvae of *A. aegypti*, was chosen as the catching station. The pots containing larvae from the other houses were brought into this house and left there throughout the series, to increase the population.

Analysis of the results follows the method used in the first paper. Times of sunrise and sunset have been taken from the tables published by the East African Meteorological Department.

Results.

The total numbers of mosquitos of all species taken in the series were as follows:—

	Females	Males
Anopheles (*Anopheles*) *coustani* var. *tenebrosus* Dön.	1	–
A. (*Myzomyia*) *funestus* Giles	2	–
A. (*M.*) *rhodesiensis* Theo.	1	–
A. (*M.*) *gambiae* Giles	2	–
Mansonia (*Mansonioides*) *africana* (Theo.)	6	–
M. (*M.*) *uniformis* (Theo.)	28	–
Aëdes (*Stegomyia*) *aegypti* (L.)	427	144
Carried forward	467	144

	Females	Males
Brought forward	467	144
A. (*S.*) *simpsoni* (Theo.)	6	–
A. (*Skusea*) *pembaensis* (Theo.)	1	–
Culex (*Culex*) *sitiens* Wied.	1	–
C. (*C.*) *tritaeniorhynchus* Giles	26	–
C. (*C.*) *univittatus* Theo.	1	–
C. (*C.*) *simpsoni* Theo.	1	–
C. (*C.*) *pipiens fatigans* Wied.	98	1
C. (*C.*) *antennatus* (Becker)	5	–
Culex sp. indet.	8	–
Totals:	614	145

Mrs. van Someren kindly examined the material and assigned the specimens of *A. aegypti* to the three forms, type form, subspecies *formosus* (Wlk.) and var. *queenslandensis* (Theo.), using the criteria of Mattingly (1957). Such separation was not always easy since, with the presence of intermediate forms, the series was graded from the darkest example of subsp. *formosus* to the palest of var. *queenslandensis*. The specimens of var. *queenslandensis* were further separated by the author into those in which the lateral spots on the abdominal tergites were metallic silver and those in which these spots were represented by patches of matt white scales. The full separation is given in Table I. These groupings are rather arbitrary: a preliminary account of the genetics of abdominal pattern variation in *A. aegypti* is in preparation. The distribution of different forms in the series was, however, independent of the hour of capture.

TABLE I.

Material of *Aëdes aegypti* from 24-hr. catches at Ganda assigned to type form, subspecies *formosus* and two groups of var. *queenslandensis*.

	Females.						Males	
	Hut compound		Hut interior		Total		Hut compound	
		%		%		%		%
var. *queenslandensis* lateral spots silver	13	(6·0)	16	(7·6)	29	(6·8)	10	(11·8)
lateral spots white	151	(69·6)	171	(81·4)	322	(75·3)	28	(32·9)
type form	43	(19·8)	19	(9·0)	62	(14·5)	37	(43·4)
subspecies *formosus*	4	(1·8)	0	(0)	4	(0·9)	5	(5·9)
Indeterminate	6	(2·8)	4	(1·9)	10	(2·3)	5	(5·9)
Totals ..	217	(100·0)	210	(99·9)	427	(99·8)	85	(99·9)

The mean hourly incidence of females of *A. aegypti* (*sensu lato*) at the bait in the hut compound and hut interior are given separately, and combined, in Table II. The curve for the combined biting incidence is given in fig. 1, B. Incidence of males is given for the hut compound alone, because after the first interior catch the team was instructed to take only those mosquitos actually biting, and

the results for compound and interior would, therefore, not be comparable. The curves for males and females in the hut compound are compared in fig. 1, A.

Despite marked variation between individual catches, and the different climatic conditions prevailing during the two series, it will be noticed that the cycles for the hut compound and interior are strikingly similar, with a very pronounced

TABLE II.

Hourly incidences of males and females of *Aëdes aegypti* in two series of ten 24-hour baited catches at Ganda.

Hour (catch time)	Hut compound						Hut interior			Combined
	Males			Females			Females			Females
	Total	No. of days	M_G as %	Total	No. of days	M_G as %	Total	No. of days	M_G as %	M_G as %
00–01	—	—	—	2	2	1·0	3	2	1·5	1·2
01–02	—	—	—	—	—	—	—	—	—	—
02–03	—	—	—	2	1	0·8	1	1	0·5	0·6
03–04	—	—	—	2	1	0·8	1	1	0·5	0·6
04–05	—	—	—	—	—	—	2	2	1·1	0·5
05–06	16	6	18·6	4	3	1·8	2	2	1·1	1·5
06–07	10	5	12·6	8	7	4·5	10	6	5·5	5·1
07–08	4	2	4·1	7	6	3·8	8	4	3·7	3·8
08–09	3	2	3·6	4	3	1·8	7	4	3·6	2·7
09–10	6	4	7·3	8	5	3·8	6	5	3·4	3·7
10–11	7	4	8·0	12	6	5·5	16	7	8·4	7·0
11–12	4	2	4·1	11	5	4·8	11	5	5·3	5·1
12–13	3	2	3·6	6	5	3·1	6	4	3·0	3·1
13–14	1	1	1·2	7	5	3·5	13	6	6·8	5·1
14–15	6	3	6·2	15	4	4·9	8	2	2·6	3·8
15–16	6	4	7·6	23	8	11·1	19	4	5·3	8·1
16–17	6	5	8·3	30	8	14·2	18	6	7·5	10·7
17–18	12	5	13·5	33	9	14·8	30	9	15·9	15·6
18–19	—	—	—	18	8	9·3	24	8	12·4	11·0
19–20	—	—	—	6	2	1·8	14	6	6·9	4·1
20–21	—	—	—	4	2	1·6	3	2	1·5	1·5
21–22	—	—	—	4	4	2·1	5	2	1·9	2·0
22–23	1	1	1·2	7	4	3·2	2	2	1·1	2·2
23–24	—	—	—	4	3	1·8	1	1	0·5	1·2

Columns give totals for each series, number of positive catches in each series of ten, and the geometric mean, calculated as a percentage.

peak in the hour before sunset. In the first and fifth hours after sunrise there are two smaller but nonetheless clearly defined peaks. There is an indication of a small peak two hours before midnight. The only obvious differences between the series are the more abrupt onset and slower decline of the afternoon peak and the presence of the small and probably spurious peak in hour 13–14 in the hut interior.

The incidence of males at the bait is seen to follow very closely that of the females, with peaks at nearly the same times, but the maximum activity is just before sunrise instead of before sunset.

Discussion: Comparison of Biting Cycles.

The present biting cycle differs from that found near Entebbe in that the single morning peak shown there in the third hour after sunrise is replaced by two distinct peaks in the first and fifth hours, respectively, after sunrise. Activity

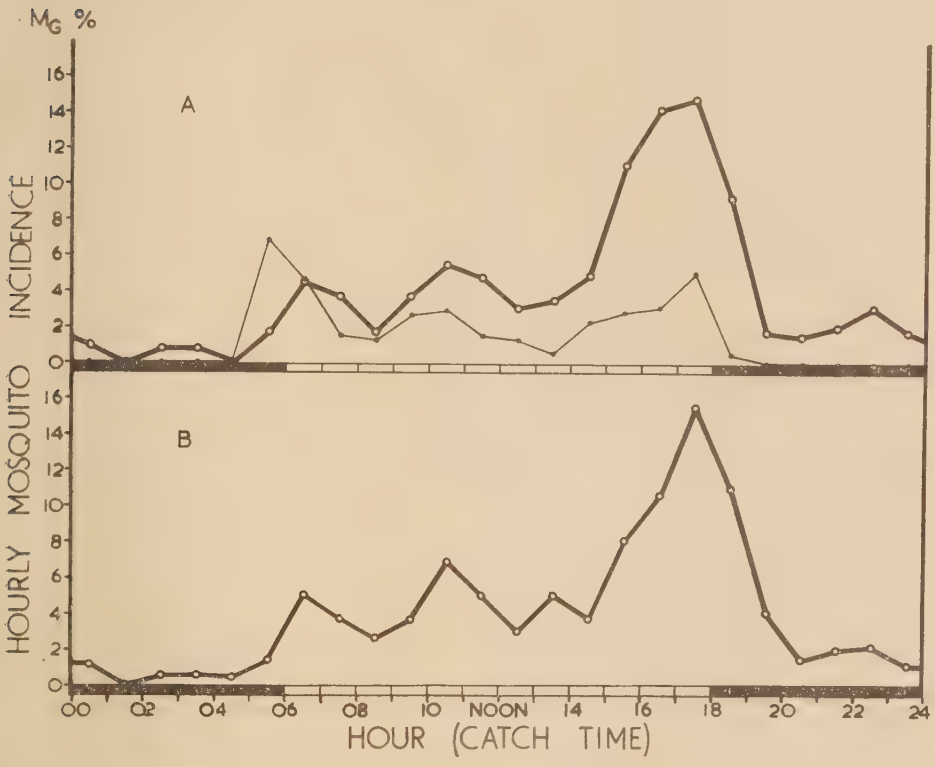


Fig. 1.—A. Biting activity of *Aëdes aegypti* (thick line) and incidence of males at the bait (thin line) in hut compound, Ganda, Kenya. Geometric means of biting activity expressed as percentages. Means for male incidence bear same numerical relation to biting means as in the catch totals. B. Biting activity of *A. aegypti* from the combined catches in the hut compound and hut interior at Ganda. Geometric means expressed as percentages.

during the morning is thus much greater, but maximum activity is still in the late afternoon with a peak in the hour before sunset, declining, during the next two hours, to a low nocturnal level.

Between sunset and sunrise 26·0 per cent. of the total females were taken. Although the proportion taken at night inside the hut (58:152) is greater than that in the compound (53:164) the difference between the series is not significant ($\chi^2 = 0{\cdot}57$ $P > 0{\cdot}30$ for n = 1). Omitting the twilight hours, 18–19 and 05–06, the percentage drops to 14·8. A further 4·7 per cent. is accounted for by hour 19–20 in which the sunset peak in the hut interior is still declining. Between 19 or 20 hr., and 05 hr. only 1·3 per cent. were taken in the Entebbe catches. Thus, allowing for the later decline of the sunset peak, nocturnal biting activity in the Ganda series is about ten times greater.

These differences are especially interesting in the light of Boorman's (1958) recent studies in Nigeria. He found biting cycles for *A. aegypti*, one in an open site between the village and plantations, and the other inside a hut, which resemble very closely those in the comparable sites at Entebbe and Ganda, respectively. In another site, among bushes in an interzone between the village and forest, there was a gradual increase in activity from sunrise to sunset. In the village centre, but outside houses, only the first of the two morning ' hut ' peaks was found. Nocturnal activity appeared to be greater in the hut and village centre than in the open sites.

Teesdale (1955) at Mombasa, and van Someren, Heisch & Furlong (1958) at Ganda, in 24-hour catches both indoors and outside extending over more than a year, took an average of less than ten females per catch, so that the numbers available for analysis are small. Nevertheless the cycles they inferred are very similar, comprising a mid-morning peak and a late afternoon or crepuscular peak, which inside the house tended to be later than outside and smaller than the morning peak. No adjustment was made for variations in the time of sunset, which would have been earliest in the fairly wet month of November and latest in the driest month of February, when populations of *A. aegypti* are unlikely to be similar in size, a factor which would cause bias. Teesdale himself gives figures showing wide monthly variations in house captures of *A. aegypti*, which were lowest in February.

The safest conclusion that may be drawn from these catches is that activity is greatest during the morning and in the late afternoon. Macdonald (1956) in a few catches in houses in Malaya, and Lumsden (1955) taking 2,594 females in a continuous 49-hour catch at Newala in southern Tanganyika both inside a hut and on the verandah, reached similar conclusions. Morlan & Hayes (1958) in southern U.S.A. found a peak of biting in the hour before sunset, but their observations were confined to the period from one-and-a-half hours before sunset to one-and-a-quarter hours after.

In a later paper, Lumsden (1957) analysed the results of his catch in detail and inferred that peaks of activity in *A. aegypti* can occur at seven times in the 24-hour period. Six of these were evident in his verandah catch and four in the contemporaneous catch inside the hut.

There are certain objections to the drawing of so detailed a conclusion from so short a catch, the catchers' unfamiliarity with method and routine, and the above-mentioned possible difference in population, excepted. The single catch will indicate the behaviour of a population with a particular age structure under particular microclimatic conditions, but unless these conditions are accurately specified, or their effects largely minimised by a number of replicates, generalisations regarding behaviour can be accepted on only the widest basis. Age structure of the population will vary unless the emergence of adults is constant from day to day, which is unlikely since most hatching of eggs will occur periodically when the water containers are filled. Lumsden places much emphasis on the coincidence of peaks of activity on the two days of the catch, but his figures show that only half the peaks were repeated in the same hour, some, moreover, being represented by only a single hour of higher activity.

In view of these considerations, it is felt that little is to be gained from Lumsden's analysis beyond his earlier conclusion of essentially bimodal activity, which is in fact demonstrated if his total figures, for the hut verandah and interior combined, are grouped in two-hour periods. Grouping of the present catch figures in a similar manner only emphasises the pattern of the raw data.

To generalise, it appears that maximum biting activity always occurs from one or two hours before sunset to just after, and where there are subsidiary peaks these occur in a series of waves of increasing intensity until the maximum is reached. This general pattern of waves is shown clearly in the curves for both

the hut compound and interior, by Boorman's curves for three sites (the fourth having only the main peak) and in Lumsden's hut interior cycle. Although the afternoon or pre-sunset peak is undoubtedly the most prominent and consistently recurring peak in all sites studied, it would be misleading to ignore the subsidiary peaks, since they may represent an integral part of biting activity.

There seems no indication of a "depletion curve" component which Colless (1957) suggests as a probable element in most biting cycles, which is interesting in view of the confined area of the present catches.

Relationship of Biting Cycle to other Activity Rhythms, and Conclusions.

Harker (1958) has stated that times of biting in the case of mosquitos should not be used as a criterion of general activity, as they form but a small (although important) part of total activity. Nevertheless, the relation of the biting cycle to rhythms of other activities, such as oviposition, is most important, as each enables at least one phase of activity to be expressed quantitatively (Gillett, Corbet & Haddow, 1959).

In the previous paper in this series (McClelland, 1959) it was noted that, at Entebbe, the cycles of biting females and males at the bait were essentially the same as those of mating and general activity and very similar to the oviposition cycle found in the laboratory by Haddow & Gillett (1957). Furthermore, the relative difference in timing between the Entebbe biting and oviposition cycles was similar to the relative difference between the biting cycle (Haddow, Gillett & Highton, 1947) and the oviposition cycle of *Aëdes* (*S.*) *africanus* (Theo.) (Gillett & Haddow, 1957). Later, Gillett, Haddow & Corbet (1959) and Gillett, Corbet & Haddow (1959) showed that the oviposition rhythm in *A. aegypti* is endogenous but its initiation requires the alternation of light and dark periods, even as little as five minutes' light in 24 hours being sufficient to trigger the rhythm.

Despite this evidence it would be unwise to conclude that *A. aegypti* shows a unified activity rhythm, since the present study shows that in the hut compound the times of maximum activity in the males and females differ by 12 hours, although times of high and low activity coincide to give a similar pattern. In each locality, onset of male activity (measured as males at the bait at Ganda and, in the absence of comparable figures, as flight activity at Entebbe) precedes onset of biting in the morning, but the onset of the evening peak of male activity follows that of the evening peak of biting. Boorman (1958) found that the maximum activity of males occurred in the afternoon inside a hut, but in the morning outside in the village. The maximum peak of biting was in the afternoon in both sites. The relation between the cycles of activity in males and females is thus far from clear and requires further investigation.

Lumsden (1955), in reviewing theories of possible mechanisms which might account for periodicity in *A. aegypti*, finds no causal relation between microclimate and the biting cycle, such as Haddow (1945) found in *Anopheles gambiae* and *Eretmapodites* spp. These workers assumed that the influence of microclimate on biting cycles is quantitative, whereas a perhaps more plausible assumption is suggested by Bugher (1949), who found that *Aëdes africanus* in the laboratory maintained an activity rhythm under constant conditions, but that changes in the microclimate caused cessation of activity rather than changes in its intensity. Wellington (1945) found minimum flight temperatures in Canadian *Culex* sp., the males having a lower threshold temperature than the females. A similar sexual difference in *A. aegypti* might account for the earlier onset of male activity.

Davies (1957) in England and Lewis (1957, 1958) in Nigeria have found that the proportion of parous and nulliparous females of two species of *Simulium*, taken biting, varies with the time of day, but this has yet to be significantly

demonstrated in mosquitos. A theory of differential biting of age-groups not only supposes a change in the diel rhythm of an individual mosquito with age, which might therefore be expected also to affect oviposition activity, but must account for as many as four or even more discrete activity peaks. Alternatively, a multi-peaked cycle may be explained by the presence of different elements (other than age-groups) in the population, each with its particular pattern of activity. Although different forms were present in the Ganda population, there is no evidence of correlated differences in the biting cycle.

Mattingly (1949) suggested that intrinsic rhythms in the mosquito, independent of the environment, might be involved, and Gillett, Corbet & Haddow (1959) consider that in biting, as well as oviposition, an endogenous 24-hour rhythm is probably a controlling factor.

The following hypothesis is suggested which, it is considered, offers an explanation for the varied forms of biting cycle observed in this species.

A. aegypti possesses an endogenous multi-peaked diel rhythm of activity. Activity impulses occur in a cycle of waves of increasing intensity reaching a maximum at the end of the daylight period. In the most favourable environment many of these impulses will result in waves of activity, which may be manifest in biting. The impulses may result in delayed or suppressed activity if microclimatic conditions, during any period, are outside the threshold limits of activity.

Thus, inside the hut there are three peaks of activity and indication of a fourth in hour 13–14, when temperature and humidity are approaching their maxima and minima, respectively (Haddow, 1942). The main peak occurs an hour later, and falls off more slowly, than in the compound, where cooler and more humid conditions will be sooner attained. In the compound there is no trace of a peak in hour 13–14, when conditions will be hotter and drier than in the hut. In the open, among vegetation, post-sunrise activity is delayed for one or two hours by the sub-threshold temperature, and a mid-morning peak suppressed by the more rapid change to hot dry conditions than in the shelter of the hut.

In short, a biting peak will result when a host-seeking or general activity impulse coincides with environmental conditions within the range between upper and lower activity thresholds.

Physiological studies are leading to a more complete understanding of the mechanisms of rhythmic activity, but the need for further field study must not be overlooked.

Summary.

Since the sharply defined biting cycle shown by outdoor populations, in Uganda, of *Aëdes aegypti* (L.), which closely resembles oviposition and general activity rhythms, could not be reconciled with the ill-defined patterns found in domestic populations, on the Kenya coast, in the absence of knowledge of the composition of the population involved there, 24-hour baited catches were made at Ganda on the Kenya coast, and the abdominal colour pattern of each individual was noted. In the series there was gradation from the darkest to the palest.

Of 427 females taken biting, 82·1 per cent. were of var. *queenslandensis* (Theo.) in the generally accepted sense, 14·5 per cent. of the type form and 0·9 per cent. of subsp. *formosus* (Wlk.). The material of var. *queenslandensis* was further divided into two groups in which the lateral spots on the abdominal tergites were of silver and matt white scales, respectively.

Very similar biting cycles, with the main peak in the hour before sunset, occurred both inside a hut and within an adjacent compound, although catches were not concurrent and were made under different seasonal conditions.

The distribution of the various colour forms in the total catch was independent of the hour of capture.

There is a resemblance between these cycles and those reported in comparable situations in Nigeria, where, with the exception of the paler forms, the population of *A. aegypti* is similar to that at Ganda. It is concluded that the main biting peak is shortly before sunset. Subsidiary peaks, when present, occur with increasing intensity as the day progresses.

The relationship of biting activity to other aspects of general activity is discussed, and it is concluded that several aspects require further investigation.

The following hypothesis is offered to account for the various patterns of biting cycle observed in different situations. It is suggested that *A. aegypti* possesses an endogenous multi-peaked diel rhythm of activity. Activity impulses occur in a cycle of waves of increasing intensity from dawn onwards, reaching a maximum at the end of the daylight period, and a biting peak will result when such an impulse coincides with environmental conditions within the range between upper and lower thresholds of activity.

Acknowledgements.

The work of which this study forms a part was wholly financed from the Colonial Development and Welfare Fund. I am indebted to the Director of the East African Virus Research Institute for the generous provision of staff and transport. I am particularly grateful to Mrs. E. C. C. van Someren of the Kenya Medical Department for so kindly examining my material, much helpful discussion and allowing me to read her recently published paper in the typescript, and to Dr. J. C. Bugher of the Rockefeller Foundation, New York, and Mr. J. P. Boorman of the Virus Research Unit, Lagos, for permission to quote from unpublished reports and to the latter also for sending material. At Ganda, my thanks are due to Mr. J. O. Harper and Mr. G. Oketch of the Kenya Medical Department for advice and assistance, and to the District Administration, Malindi.

References.

Boorman, J. P. T. [1958]. Studies on the biting habits of adult mosquitoes at Ilobi.—*Rep. W. Afr. Coun. med. Res. 1957* pp. 34–96.

Bugher, J. C. [1949]. Responses of mosquitoes to changes in microclimate.—*Rep. Yell. Fever Res. Inst. Lagos 1948* pp. 166–175.

Colless, D. H. (1957). Components of the catch curve of *Culex annulus*.—*Nature, Lond.* **180** pp. 1496–1497.

Davies, L. (1957). Study of the age of females of *Simulium ornatum* Mg. (Diptera) attracted to cattle.—*Bull. ent. Res.* **48** pp. 535–552.

Gillett, J. D., Corbet, P. S. & Haddow, A. J. (1959). Observations on the oviposition-cycle of *Aëdes* (*Stegomyia*) *aegypti* (Linnaeus), III.—*Ann. trop. Med. Parasit.* **53** pp. 132–136.

Gillett, J. D. & Haddow, A. J. (1957). Laboratory observations on the oviposition-cycle in the mosquito *Aëdes* (*Stegomyia*) *africanus* Theobald.—*Ann. trop. Med. Parasit.* **51** pp. 170–174.

Gillett, J. D., Haddow, A. J. & Corbet, P. S. (1959). Observations on the oviposition-cycle of *Aëdes* (*Stegomyia*). *aegypti* (Linnaeus), II.—*Ann. trop. Med. Parasit.* **53** pp. 35–41.

Haddow, A. J. (1942). The mosquito fauna and climate of native huts at Kisumu, Kenya.—*Bull. ent. Res.* **33** pp. 91–142.

HADDOW, A. J. (1945). The mosquitoes of Bwamba County, Uganda. II. Biting activity with special reference to the influence of microclimate.—*Bull. ent. Res.* **36** pp. 33–73.

HADDOW, A. J. (1954). Studies of the biting-habits of African mosquitoes. An appraisal of methods employed, with special reference to the twenty-four-hour catch.—*Bull. ent. Res.* **45** pp. 199–242.

HADDOW, A. J. & GILLETT, J. D. (1957). Observations on the oviposition-cycle of *Aëdes* (*Stegomyia*) *aegypti* (Linnaeus).—*Ann. trop. Med. Parasit.* **51** pp. 159–169.

HADDOW, A. J. GILLETT, J. D. & HIGHTON, R. B. (1947). The mosquitoes of Bwamba County, Uganda. V. The vertical distribution and biting-cycle of mosquitoes in rain-forest, with further observations on microclimate.—*Bull. ent. Res.* **37** pp. 301–330.

HARKER, J. E. (1958). Diurnal rhythms in the animal kingdom.—*Biol. Rev.* **33** pp. 1–52.

LEWIS, D. J. (1957). Aspects of the structure, biology and study of *Simulium damnosum*.—*Ann. trop. Med. Parasit.* **51** pp. 340–358.

LEWIS, D. J. (1958). Observations on *Simulium damnosum* Theobald at Lokoja in Northern Nigeria.—*Ann. trop. Med. Parasit.* **52** pp. 216–231.

LUMSDEN, W. H. R. (1952). The crepuscular biting activity of insects in the forest canopy in Bwamba, Uganda. A study in relation to the sylvan epidemiology of yellow fever.—*Bull. ent. Res.* **42** pp. 721–760.

LUMSDEN, W. H. R. (1955). An epidemic of virus disease in Southern Province, Tanganyika Territory, in 1952–53. II. General description and epidemiology.—*Trans. R. Soc. trop. Med. Hyg.* **49** pp. 33–57.

LUMSDEN, W. H. R. (1957). The activity cycle of domestic *Aëdes* (*Stegomyia*) *aegypti* (L.) (Dipt., Culicid.) in Southern Province, Tanganyika.—*Bull. ent. Res.* **48** pp. 769–782.

MCCLELLAND, G. A. H. (1959). Observations on the mosquito, *Aëdes* (*Stegomyia*) *aegypti* (L.), in East Africa. I. The biting cycle in an outdoor population at Entebbe, Uganda.—*Bull. ent. Res.* **50** pp. 227–235.

MACDONALD, W. W. (1956). *Aëdes aegypti* in Malaya. II. Larval and adult biology.—*Ann. trop. Med. Parasit.* **50** pp. 399–414.

MATTINGLY, P. F. (1949). Studies on West African forest mosquitos. Part II. The less commonly occurring species.—*Bull. ent. Res.* **40** pp. 387–402.

MATTINGLY, P. F. (1957). Genetical aspects of the *Aëdes aegypti* problem. I. Taxonomy and bionomics.—*Ann. trop. Med. Parasit.* **51** pp. 392–408.

MORLAN, H. B. & HAYES, R. O. (1958). Urban dispersal and activity of *Aëdes aegypti*.—*Mosq. News* **18** pp. 137–144.

VAN SOMEREN, E. C. C., HEISCH, R. B. & FURLONG, M. (1958). Observations on the behaviour of some mosquitos of the Kenya coast.—*Bull. ent. Res.* **49** pp. 643–660.

TEESDALE, C. (1955). Studies on the bionomics of *Aëdes aegypti* (L.) in its natural habitats in a coastal region of Kenya.—*Bull. ent. Res.* **46** pp. 711–742.

WELLINGTON, W. G. (1945). The effect of ground temperature inversions upon the flight activity of *Culex* sp. (Diptera, Culicidae).—*Canad. Ent.* **76** p. 223.

© Commonwealth Agricultural Bureaux, 1959.

THE OVIPOSITION AND DURATION OF LIFE OF A SMALL STRAIN OF THE RICE WEEVIL, *CALANDRA ORYZAE* (L.), IN SIERRA LEONE.

By P. F. Prevett, B.Sc., A.R.C.S., D.I.C.

Pest Infestation Laboratory, Slough.

In Sierra Leone, *Calandra oryzae* (L.) is a major primary pest of parboiled milled rice and native cleaned rice (that is, rice hand-pounded after native parboiling of paddy). During a three-year study of problems of infestation of stored paddy and rice in that territory (Prevett, *in press*), laboratory-scale experiments were carried out to obtain data on certain pests under the local climatic conditions. Observations on the susceptibility of rice in its various forms to attack by the rice weevil, and on the effect of grain moisture-content on its development are discussed elsewhere (Prevett, *in press*).

Two strains of the rice weevil are recognised, and Richards (1944) showed that they could be readily distinguished by size. On this basis it is considered that the weevils used in the present work belonged to the small strain. Recent work by E. H. Floyd and L. D. Newsom at the Louisiana Agricultural Experiment Station (unpublished, 1958) has established further morphological differences between the strains, including differences in both male and female genitalia, and these workers conclude that the strains merit recognition as separate species, the larger strain as *Calandra oryzae* (L.) and the smaller as *C. sasakii* Tak. Observations made on the oviposition and duration of life of the small strain are described below.

The experiment was carried out during the period May–August 1955, under normal conditions of temperature and relative humidity. The moisture content of the rice used was 13·0 per cent. It is, however, considered probable that after exposure in the experimental tubes to the diurnal variation in relative humidity the moisture content of the surface of the grains was lower. This possibly has some bearing on the results discussed below, and it is for this reason that the

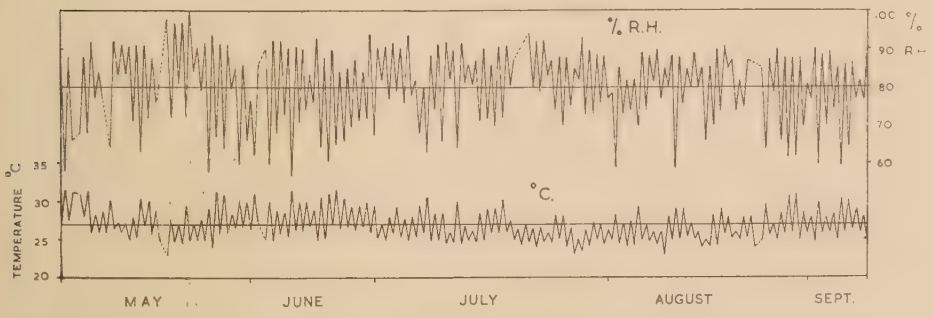


Fig. 1.—Laboratory conditions of temperature and relative humidity. Daily maxima and minima, May—September 1957.

Horizontal lines denote means.

physical conditions are illustrated in the detail shown in fig. 1, the observations made by most other workers on this species having been made under controlled conditions. It must be pointed out that these graphs are intended to give only a general picture of the variation which took place in the laboratory during the course of the experiment, as the data used have been taken from thermohygrograph records for the appropriate period in 1957. It is unfortunate that such records are not available for 1955, but a comparison of whirling hygrometer readings taken daily at 11 a.m. in 1955, with thermohygrograph readings at 11 a.m. in 1957 shows that there is no great difference between the two years (see Table I).

TABLE I.

Monthly mean temperature and relative humidity at 11 a.m. for the years 1955 and 1957.

Month	1955				1957			
	Temp. (°C.)		R.H. (%)		Temp. (°C.)		R.H. (%)	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean
May ..	25·0–32·0	28·9	66–81	73·3	25·0–32·0	27·7	64–94	77·7
June ..	25·0–29·8	27·1	72–85	79·8	26·5–29·5	28·3	65–84	76·3
July ..	23·0–28·3	26·4	68–92	81·7	24·5–28·0	26·4	75–88	81·1
Aug. ..	24·4–29·0	25·9	69–92	83·3	25·0–29·0	26·5	62–89	77·3
Mean		27·1		79·5		27·2		78·1

The mean maximum and minimum temperatures over the period illustrated in fig. 1 were 28·6 and 25·4°C. (ranges 25·0–31·5°C. and 23·0–28·0°C., respectively), and the mean maximum and minimum relative humidity 88·6 per cent. and 71·4 per cent. (ranges 77–99 per cent. and 57–85 per cent., respectively). The mean temperature of 27°C. and mean relative humidity of 80 per cent. are indicated by the horizontal lines in fig. 1.

Methods.

One pair of freshly-emerged adults of *C. oryzae* was placed in each of twenty 3″ × 1″ specimen tubes, each with ten grains of parboiled milled rice (sterilised at 70°C. for five hours, and allowed to reach equilibrium with the ambient relative humidity). Sexing of weevils was carried out by examining the dorsal surface of the rostrum, which is much more closely and strongly punctured in the male than in the female (Richards, 1947).

Every two days the rice was changed and the number of eggs laid during the two-day period determined. The grains were soaked in 50 per cent. alcohol for 24 hours (as described by Howe, 1952), and then examined under the microscope, each grain being cut longitudinally. In this way, the above treatment having rendered the grain soft and to a certain degree translucent, it is possible to dissect out the eggs from the grain. This eliminates the possibility of counting egg-plugs beneath which there are no eggs, a source of error inherent in some other methods.

Male weevils were left with females throughout the period of the experiment. On a few occasions males were found to have died during the preoviposition period, or early oviposition period, and were replaced. All weevils used were obtained every other day by sieving from cultures maintained on parboiled milled rice under the same conditions of temperature and relative humidity as in this experiment.

Results and Discussion.

The results obtained are summarised in Table II and the oviposition rate is illustrated in fig. 2, the values for tubes numbered 2 and 20 having been omitted in the calculation of means for the graph in view of the abnormally low numbers of eggs recorded from these tubes. Numbers laid per six-day period have been plotted in order that some comparison may be made with the results of other workers, which are expressed in terms of eggs laid per week (Birch, 1945*b*), or per 14 days (Segrove, 1951).

On average the total number of eggs laid per female was 62 (or 68 omitting records from tubes 2 and 20), which is estimated to represent an approximate rate of one egg per female per day over the oviposition period. Results obtained by Nakayama (1941) under similar conditions of temperature and relative humidity are comparable. He records that the number of eggs laid by females kept at 26–27°C. and 80–85 per cent. R.H. averaged 68·75. Fifty-six per cent. of females laid 50–90 eggs (as compared with 65 per cent. in the present work), and 10 per cent. laid over 100 eggs (as compared with 10 per cent. in the present work).

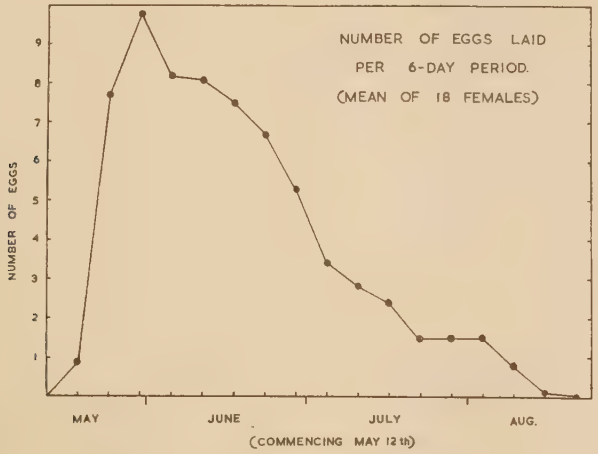


Fig. 2.—*Calandra oryzae*: oviposition rate.

The rate of egg-laying rose to a peak which was reached during the third week and thereafter gradually declined. A similar pattern is recorded by Birch (1945*a*), who states that the maximum rate of egg-laying occurs at the end of the first or second week, depending on the temperature, and that egg-laying continues for about three months at temperatures above 23°C. In the present work the mean preoviposition period (see Table II) was 6 days and, omitting the records from tubes 2 and 20, the oviposition period and postoviposition period 71 and 22 days, respectively. The highest number of eggs laid in any two-day period was seven, the mean of the highest numbers for the 20 weevils being approximately five.

Usually only one egg was laid per grain, but sometimes two or three, and on one occasion even four, were laid together. It is evident from fig. 3 that, of all the grains presented to the weevils throughout the experiment, 87 per cent. were not utilised for oviposition. The 13 per cent. of grains utilised is indicated by

the blank triangle, and can be split into grains on which two or three eggs were laid, as illustrated. It has been calculated that 81 per cent. of the eggs laid were laid singly, 16·8 per cent. were laid as one of two on a grain and 2·2 per cent. as one of three, as illustrated in the second graph of fig. 3. Treĭman (1937) states that, on unpolished rice, eggs are usually laid singly, but up to four larvae may occur in a grain. In Sierra Leone the final product of milling, as used in this experiment, can be described as unpolished or undermilled rice, streaks of bran being present in grooves on the grains.

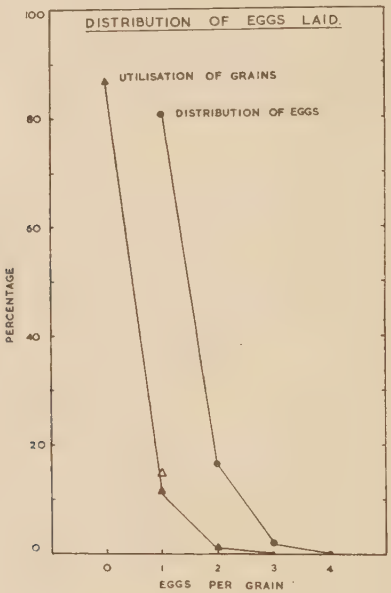


Fig. 3.—*Calandra oryzae*: distribution of eggs laid.

The numbers of eggs laid in this experiment are considerably lower than those recorded for *C. oryzae* by some other workers, and were recorded under conditions of temperature and relative humidity the mean values of which were close to the optima for the species. Dendy & Elkington (1920) state that the optimum temperature is 28°C., and Birch (1945*a*) shows that oviposition is at its highest rate at temperatures between 25·5 and 29°C. There are several factors which are considered to have some bearing on this low rate of oviposition.

First, in contrast to this experiment, a great deal of the experimental work of *C. oryzae* has involved the use of wheat, a very much softer medium for oviposition than rice. Dendy & Elkington (1920) state that the rate of oviposition of this species depends on the hardness of the grain, and this would seem to gain support from the results of Sandner (1959), who records that a very small number of eggs was laid by the rice weevil on rice and oats, as compared with rye, wheat and barley. Some figures given by Birch (1945*b*) are also relevant. In an experiment with wheat of different moisture contents, 344 eggs were laid on wheat at 14 per cent. moisture content, whereas only 75 eggs were laid on wheat at 12 per cent. moisture content. It is suggested that this effect of moisture content is in relation to the hardness of the grain.

Secondly, it would appear that a difference in oviposition potential exists between the two strains of *C. oryzae*. Segrove (1951) records that at 25°C. and 70 per cent. R.H. the fecundity of the large strain is about 50 per cent. higher than that of the small strain. This is in agreement with Richards (1944).

Finally, Howe (1952) and Birch (1945*b*) have shown that the density of weevils in relation to the quantity of grain has an important bearing on the rate

TABLE II.

Oviposition and duration of life of *Calandra oryzae*.

Tube No.	Total no. of eggs laid	Daily mean no. of eggs laid	No. of times two eggs were laid on a grain	No. of times three eggs were laid on a grain	No. of times four eggs were laid on a grain	Highest no. of eggs laid in a two-day period	Preoviposition period (days)	Oviposition period (days)	Postoviposition period (days)	Duration of life (days)	
										Male	Female
1	58	1·05	7	—	—	5	6	55	5	66	66
2	11	1·83	1	—	—	5	6	6	2	14*	14*
3	74	1·16	7	—	—	7	6	64	18	76	88
4	48	0·77	2	—	—	5	6	62	14	94	82
5	107	1·27	12	2	1	7	6	84	60	166	150
6	74	0·88	6	2	—	5	4	84	46	150	134
7	61	0·73	1	—	—	3	6	84	4	82	94
8	51	0·67	4	—	—	4	8	76	36	120	120
9	56	1·27	5	—	—	6	4	44	10	72	58
10	73	1·04	7	—	—	5	4	70	14	52	88
11	88	1·07	7	2	—	5	4	82	46	132	132
12	87	1·04	8	1	—	5	4	84	4	102	92
13	47	0·64	5	—	—	4	10	74	74	188	158
14	60	0·79	4	—	—	5	8	76	10	114	94
15	54	0·69	2	—	—	4	4	78	10	140	92
16	114	1·27	13	2	—	7	4	90	6	112	100
17	47	0·65	1	—	—	4	6	72	8	158	86
18	60	1·50	7	—	—	5	6	40	18	158	64
19	57	1·10	5	—	—	5	6	52	20	108	78
20	5	0·19	—	—	—	1	8	26	118	164	152
Mean	61·6	0·99	5·2	0·5	0·1	4·8	5·8	65·2	26·2	113·4	97·1

* Died in copula.

of oviposition. Howe states that maximum egg-laying is not attained unless many grains are available for oviposition. It is considered, therefore, that the percentage utilisation of grains recorded in this experiment cannot serve as a guide to the degree of infestation by the rice weevil to be expected in storage of milled rice.

With regard to length of life, a ' t ' test of significance of difference of means applied to the figures given in Table II indicates that there is no significant difference in the number of days for which male and female weevils lived, the mean figures being 113 and 97, respectively.

Summary.

A study has been made of the rate of oviposition, on parboiled milled rice, of the small strain of the rice weevil, *Calandra oryzae* (L.), under normal laboratory conditions of temperature and relative humidity (means 27°C., 80% R.H.) in Sierra Leone, and of the utilisation of grains for oviposition.

On the average, a female laid 68 eggs in all, over an oviposition period of 71 days, the peak of egg-laying being reached during the third week. Only 13 per cent. of grains were utilised. Differences between the results obtained and those recorded by previous workers are discussed.

The mean length of life of male and female weevils was found to be 113 and 97 days, respectively.

Acknowledgements.

My thanks are due to the Director of Commerce & Industry, Freetown, Sierra Leone, in whose Department this work was carried out; to the Director, Pest Infestation Laboratory, D.S.I.R., for so kindly allowing me the facilities of the Laboratory during the preparation of this paper; to Dr. D. W. Hall, Mr. R. W. Howe and Mr. M. E. Solomon for their advice and criticism; and to Dr. E. H. Floyd and Dr. L. D. Newsom for permission to refer to unpublished work.

References.

Birch, L. C. (1945*a*). A contribution to the ecology of *Calandra oryzae* L. and *Rhizopertha dominica* F. (Coleoptera) in stored wheat.—*Trans. roy. Soc. S. Aust.* **69** pp. 140–149.

Birch, L. C. (1945*b*). The influence of temperature, humidity and density on the oviposition of the small strain of *Calandra oryzae* L. and *Rhizopertha dominica* Fab. (Coleoptera).—*Aust. J. exp. Biol. med. Sci.* **23** pp. 197–203.

Dendy, A. & Elkington, H. D. (1920). Report on the vitality and rate of multiplication of certain grain insects under various conditions of temperature and moisture.—*Rep. Grain Pests Comm. roy. Soc.* no. 7, 52 pp.

Howe, R. W. (1952). The biology of the rice weevil, *Calandra oryzae* (L.).—*Ann. appl. Biol.* **39** pp. 168–180.

Nakayama, S. (1941). On the number of eggs laid by *Calandra oryzae* L. at constant temperature. [*In Japanese.*]—*Rep. Ass. Adv. Sci. Japan* **16** pp. 117–119. (*Rev. appl. Ent.* (A) **30** p. 8.)

Prevett, P. F. (*in press*). An investigation into storage problems of rice in Sierra Leone.—*Colon. Res. Study.* London, Colon. Off., H.M.S.O.

Richards, O. W. (1944). The two strains of the rice weevil, *Calandra oryzae* (L.) (Coleopt., Curculionidae).—*Trans. R. ent. Soc. Lond.* **94** pp. 187–200.

Richards, O. W. (1947). Observations on grain-weevils, *Calandra* (Col., Curculionidae). I. General biology and oviposition.—*Proc. zool. Soc.* **117** pp. 1–43.

Sandner, H. (1959). Studies on the ecology and behaviour of the grain weevil (*Calandra granaria* L.) and the rice weevil (*Sitophilus oryzae* L.): vertical distribution and food relations.—*Proc. XVth int. Congr. Zool. 1958* pp. 761–762.

Segrove, F. (1951). Oviposition behaviour in the two strains of the rice weevil, *Calandra oryzae* Linn. (Coleopt., Curculionidae).—*J. exp. Biol.* **28** pp. 281–297.

Treĭman, F. S. (1937). On the morphology and biology of *Calandra oryzae* L. [*In Ukrainian with English & Russian summaries.*]—*Trav. Inst. Zool. Biol. Acad. Sci. Ukr.* **14** pp. 259–277.

THE SIMULIIDAE (DIPTERA) OF BRITISH HONDURAS.*

By D. J. Lewis †

Scientific Staff, Medical Research Council, London

and

P. C. C. Garnham

London School of Hygiene and Tropical Medicine.

Man-biting Simuliids have long been known in British Honduras under the name of 'batlas', and we recently took the opportunity of collecting some specimens during visits to several parts of that country between 9th January and 15th February 1958 (fig. 1). We identified rather more than 900, namely 245 caught adults, some bred ones, and 648 pupae or their skins—280 from the Mountain Pine Ridge, 136 from the El Cayo area, and 232 from the Caves Branch–Stann Creek area (Table I). We (Garnham & Lewis, 1959) found that at the time of our visit two species were a serious pest owing to the intense irritation caused, particularly to newcomers, by their bites. In view of the prevalence of human onchocerciasis, which gives rise to a considerable amount of blindness, some 300 kilometres away, in Guatemala (fig. 1), we considered the possibility that the disease might become established in British Honduras. It appeared that a few infected people had come to the country in the past, but the Medical Department had no recent records of cases and we found none in a survey in the Stann Creek valley. It may be that infected immigrants have been too few to establish the disease, or that conditions are unsuitable for it. The country is much lower than the infected parts of Guatemala, and, of the two common anthropophilic species of *Simulium*, one is a vector of secondary importance in Guatemala, and the potentialities of the other are unknown. Agricultural development and the building of new roads will allow people to settle in *Simulium* areas which are now scarcely inhabited, but it is not possible to say if there will be any risk from onchocerciasis until more is known of the epidemiology of the disease in Central America.

Notes on the Species found.

It is not generally agreed whether the genus *Simulium* should be divided into subgenera or simply into species groups. We do not wish to express an opinion on this matter but follow here the system of Dalmat (1955), Vargas, Martínez Palacios & Díaz Nájera (1946) and Vargas & Díaz Nájera (1957, 1958) for the sake of uniformity.

Thirteen species were found, of which we prefer to leave four unnamed until more material is obtained. The known distribution in British Honduras of each species is either given below or shown in Table I. Most of the eastern localities are situated on the Humming-bird Highway.

While collecting adults biting, we found that Chloropids settling on the skin

* A grant from the Colonial Development and Welfare Fund, awarded by the Colonial Office, helped to finance this work.

† Care of British Museum (Natural History).

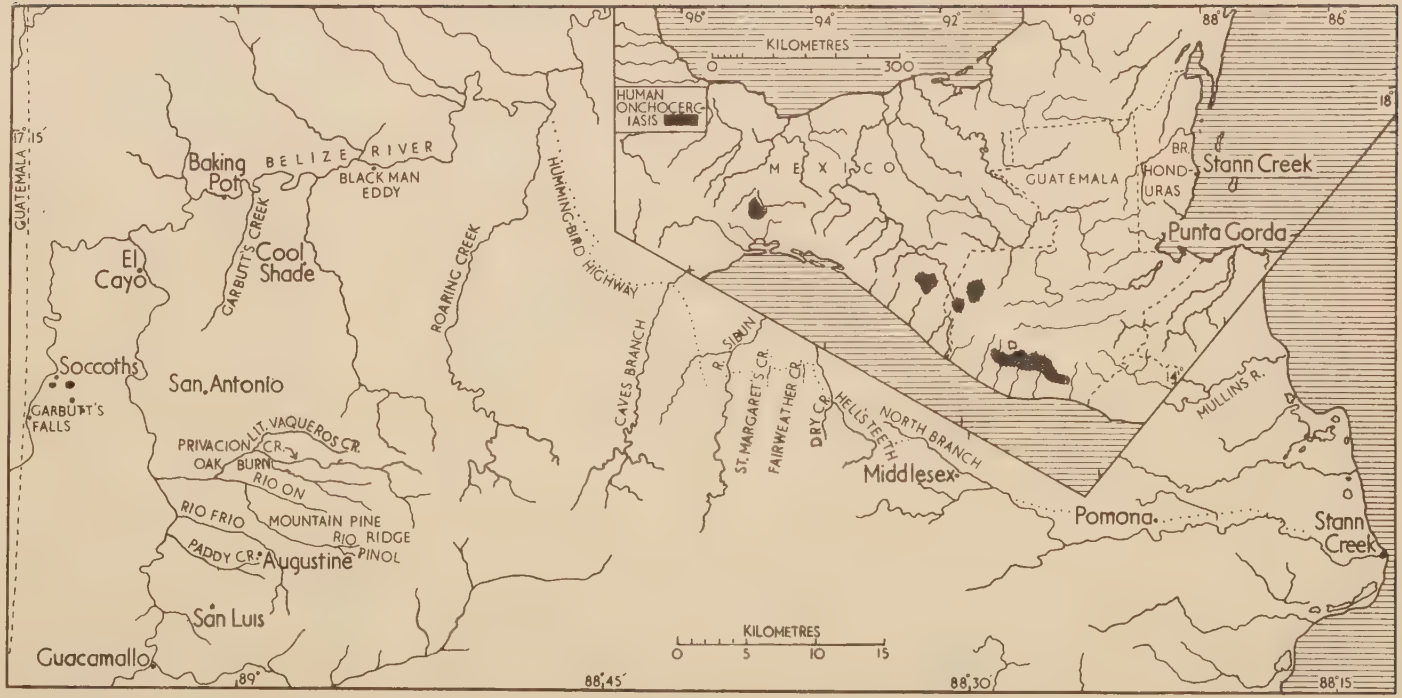


Fig. 1.—Map of part of British Honduras, showing localities mentioned in the text, and the position of British Honduras in relation to Central American areas of onchocerciasis.

were a hindrance, though a very minor one, because untrained collectors mistook them for Simuliids.

Simulium (*Byssodon*) *quadrivittatum* Lw.

This is a small black species with two longitudinal white-pruinose bands on the mesonotum and other pale markings, which was described in 1862. Figures of the pupal gills are given by Bradt (1932), Fairchild (1940, as *S. haematopotum* Malloch), Malloch (1914, as *S. metallicum* Bellardi) and Pinto (1932, as *S. metallicum* Bellardi). They resemble the gills of several other species in possessing eight slender filaments, and must therefore be carefully examined during a survey of breeding places. Vargas (1945) gives a useful bibliography of this species, with seven synonyms, and records it existence in Costa Rica, Cuba, Jamaica, Mexico, Panama, Puerto Rico and Venezuela. It is also known from two provinces of Ecuador, where it bites man but does not seem to be very common (León & Wygodzinsky, 1953). It occurs in several parts of Mexico (Vargas, Martínez Palacios & Díaz Nájera, 1946; Vargas & Díaz Nájera, 1957), but has not been found in Guatemala, where a related species, *S. benjamini* Dalmat, has been discovered in two localities on the Atlantic watershed (Dalmat, 1952, 1955). Fairchild (1940) refers to specimens of *Simulium* from British Honduras (as possibly *S. haematopotum*) which may have been *S. quadrivittatum* though they were somewhat larger than Panama material of what he wrongly identified as *S. haematopotum* Malloch.

Several authors have reported that *S. quadrivittatum* bites man. Roubaud (1906) recorded " this beautiful Cuban species " from Costa Rica, where it was a veritable plague in the hills, particularly during the rains, and he stated that, after a fly had bitten, red coagulated blood remained beneath the skin and formed a conspicuous spot which persisted for about a fortnight. Surcouf & Gonzales-Rincones (1911) quoted these observations, and Malloch (1914) reported that the species bit in Puerto Rico. Bradt (1932) published some observations on the biting and other habits of *S. quadrivittatum* in that country, and noted that scabs often lasted for a week, that local people experienced little irritation or swelling, and that he usually found the pupae on water-plants. He quoted one observer who noted that after the swelling from a bite had subsided a small area resembling a slight burn remained. Bradt saw this species biting horses but not cattle. Dunn (1934), found that *S. quadrivittatum* was very annoying in the south-west of Panama, and Fairchild (1940) wrote from Panama: " This is the only species which seems to bite man at all readily at lower elevations on the Isthmus. During the latter part of the rainy season it becomes quite annoying at . . . Juan Mina on the Chagres River. . . ." Dampf (1943) reported that in Mexico this species was confined to the tributaries of the river Coatzacoalcos near the Gulf of Mexico where it attacked man with the same persistence as did *S. haematopotum* in the basin of the River Balsas on the Pacific side of the country. Ortiz (1944) found that *S. quadrivittatum* was very voracious in western Venezuela where it bit people and donkeys. Among specimens in the British Museum are some collected at Suretka in Costa Rica on 22nd April 1917. The collector (C. B. Williams, personal communication 1958) noticed that they bit, without causing pain, but produced a small swelling at the centre of which was a red spot of clotted blood which persisted, after three days, in a small hard swelling, and was still visible after ten days.

In the parts of British Honduras which we visited, adults of *S. quadrivittatum* appeared to occur almost everywhere except in certain forest areas; specimens were identified from El Cayo, Cool Shade, Rio Frio, Hell's Teeth, Little Vaqueros Creek area, Middlesex, North Branch, Privacion Creek and the River Sibun. The abundance of this species in the inland part of British Honduras and its apparent absence or rarity in Guatemala, together with the above-

mentioned records from the literature, suggest that it tends to flourish among hills of moderate height.

Simulium (*Psilopelmia*) *callidum* (D. & S.).

This is one of the species which, like *S.* (*Simulium*) *ochraceum* Wlk. (not so far recorded from British Honduras), have an orange-yellow mesonotum. Each pupal gill has eight filaments, as in many species, but they are arranged in a characteristic manner (Dalmat, 1955, fig. 284).

In Guatemala, according to Dalmat (1955), *S. callidum* bites man, in a hesitant manner, but much less commonly than do *S. ochraceum* and *S. metallicum*, and, as a vector of *Onchocera*, is regarded as of little importance. It was not taken on human beings in British Honduras.

Simulium (*Psilopelmia*) *samboni* Jennings.

This species, which is rather similar to *S. callidum* in the adult stage, is known to occur in Guatemala (Dalmat, 1955) and in Chiapas and other parts of Mexico (Vargas & Díaz Nájera, 1951). It was not practicable to examine every single pupa in minute detail so, as indicated in Table I, it is possible that a few pupae grouped with *S. samboni* may have belonged to a closely related species. Some pupae from the Rio Frio were on a species of Podostemaceae, a group of plants not listed by Dalmat (1955).

Simulium (*Psilopelmia*) *veracruzanum* Vargas, Martínez & Díaz.

A single female, taken biting man at Ritchie's farm near Pomona, and the only one available, appears to belong to this species although the arms of the genital fork are rather broader than those depicted by Dalmat (1955). According to him, this species is widely distributed in Guatemala, bites man, and is believed to transmit onchocerciasis.

Other species of the subgenus *Psilopelmia*.

Pupae of three other species, possibly of this subgenus, were obtained. Pupae, apparently representing two species from Garbutt's Creek bear some resemblance to those of *S. dugesi* Vargas, Martínez & Díaz, and those from Hinkson's Creek (near Hell's Teeth) to a species rather like *S. ochraceum*.

The subgenus *Hemicnetha*.

S. earlei Vargas, Martínez & Díaz, *S. mexicanum* Bellardi, *S. pulverulentum* Knab, *S. virgatum* Coq. and *Simulium* sp. were identified from adults or pupae. The mesonotum of the male of *S. earlei* was rather darker than in Dalmat's description. *S. pulverulentum* is already known from Punta Gorda, the type locality, in the south of the country.

Simulium (*Simulium*) *metallicum* Bellardi.

This common biting species is easily distinguished from *S. quadrivittatum* by its slightly larger size and the absence of silvery thoracic stripes. According to Vargas (1945) it occurs in Costa Rica, Guatemala, Mexico, Panama, Trinidad and Venezuela. Dalmat (1955), who made numerous observations on this species in Guatemala, found that it was widely distributed at many different altitudes, bred in various types of stream, and bit man in larger numbers than any other species although it prefers to bite cattle and horses. He regarded it as a good secondary vector of *Onchocerca volvulus*.

In British Honduras, *S. metallicum* has been found at Fairweather Creek, Hell's Teeth, Middlesex, Pomona, St. Margaret's Creek, R. Sibun and places mentioned in Table I.

The appearance of some of the internal organs of examples of the African species, *S. damnosum* Theo., is a very useful guide to their physiological condition, and we took the opportunity of dissecting a few females of *S. metallicum* to examine some of these organs. No peritrophic membrane was noticed in the mid-gut of an individual which had sucked blood four hours before, so the membrane is presumably very delicate in this species. The Malpighian tubes are markedly moniliform—more so than in *S. quadrivittatum*—except for

TABLE I.

The numbers of pupae and pupal skins of species of *Simulium* collected in various localities.

Locality	Species												
	quadrivittatum	*callidum*	*samboni* (and others ?)	*veracruzanum*	sp.	sp.	sp.	*euclei*	*mexicanum*	*pulverulentum*	*virgatum*	sp.	*metallicum*
MOUNTAIN PINE RIDGE													
Augustine	–	–	1	–	–	–	–	–	–	–	–	–	–
Rio Frio	–	–	5	–		–	11	–	–	–	–	–	–
Rio Frio, in cave	–	–	–	–	–	–	–	–	–	–	–	–	–
Guacamallo	–	–	–	–		–	–	–	–	1	–	–	–
Little Vaqueros Creek	–	63	–	–		–	–	–	–	–	–	–	27
Little Vaqueros Creek tributary	11	8	–	–		–	–	–	–	–	–	–	32
Oak Burn	–	2	–	–		–	–	–	1	1	–	–	–
Rio On	–	–	8	–	–	–	2	–	–	4	–	–	1
Paddy Creek	–	–	5	–	–	–	–	–	–	–	–	–	3
Rio Pinol	–	55	–	–	–	–	–	3	–	–	–	–	3
Privacion Creek	–	–	1	–	–	–	–	–	–	–	–	–	17
San Luis	–	4	–	–	–	–	–	–	–	–	–	–	9
Totals (as %)	3·9	47·1	7·1	0	0	0	4·6	1·1	0·4	2·1	0·7	0	32·9
EL CAYO AREA													
Garbutt's Creek	–	–	–	–	–	3	–	–	–	2	–	–	–
Garbutt's Falls	–	–	–	–	–	–	1	–	–	56	–	–	–
San Antonio	3	–	–	–	–	–	–	–	–	–	–	–	1
Soccoths	–	–	–	–	–	–	–	–	–	69	–	1	–
Totals (as %)	2·2	0	0	0	0	2·2	0·7	0	0	93·4	0	0·7	0·7
CAVES BRANCH—STANN CREEK AREA													
Caves Branch	–	–	1	–	–	–	–	–	–	2	–	–	–
Dry Creek	–	4	83	–	–	–	–	–	–	–	–	–	–
Fairweather Creek	–	4	9	–	–	–	–	–	–	–	–	–	–
Hell's Teeth	–	24	34	–	–	–	–	–	25	–	3	–	–
Hinkson's Creek	–	–	–	–	1	–	–	–	–	–	–	–	–
Middlesex	–	–	6	–	–	–	12	–	–	–	–	–	–
North Branch	–	–	6	–	–	–	–	–	–	–	–	–	7
R. Sibun	–	–	–	–	–	–	–	2	–	9	–	–	–
Totals (as %)	0	13·8	59·9	0	0·4	0	5·2	0·9	10·8	4·7	1·3	0	3·0

the third of their length near the gut. The blind end of each tube is narrow and contains yellow material, most of the tube usually contains a pale pink substance, and the part near the gut sometimes contains purple granules. In several parous flies, the tubes were transparent as they are in older examples of *S. damnosum*. The central fat-body, part of which lies near the oviducts, was very small in some nulliparous flies, being less than a tenth the size of the head. In some parous flies, the abdominal wall had a transparent look, like older specimens of *S. damnosum*, possibly owing to the movement of chromatophores. The ovaries are so small that they are difficult to spread out, but the follicular remains, which are quite large, can easily be seen if one per cent. of a detergent is added to the dissection medium so that the oocytes disintegrate. The largest undeveloped oocyte in the ovariole of a parous fly was 0·05 mm. long and a

mature relict egg was 0·185 mm. long. In parous flies, the distal funicle of an ovariole had a beaded appearance rather like that seen in *Anopheles gambiae* Giles (Lewis, 1958).

Distribution.

Few biting Simuliids were noticed in the western forest area except near the edge of the Mountain Pine Ridge.

S. quadrivittatum was abundant at many points in the Mountain Pine Ridge; possibly it was numerous all over the area or the open nature of the vegetation enabled it to move about and attack in large numbers. The absence of *S. metallicum* in collections of biting adults in this area may have been due to insufficient collecting.

Simuliids were not very troublesome in the El Cayo area during our visit; they were, however, noticeable at Black Man Eddy and occasionally at Cayo itself, but few were seen on the Western Branch of the Belize River. There are few small streams, and the dominant species breeding in the river is *S. pulverulentum*.

In the Caves Branch—Stann Creek area, biting Simuliids, mainly *S. metallicum*, were abundant. The coastal town of Stann Creek, unlike Belize, harboured a few biting adults.

Breeding Places.

Although it is easy to find the early stages of many species of *Simulium*, it is very difficult, owing to the unusual breeding sites adopted, to locate those of some others, a notable example in the past having been the African *S. neavei* Roubaud.

S. quadrivittatum in British Honduras seems to be another example. Although it was almost ubiquitous, abundant on the Mountain Pine Ridge, and common in the Stann Creek valley, only two per cent. of the total pupae and pupal skins collected and only four per cent. of those from the Mountain Pine Ridge were of *S. quadrivittatum*. The only two breeding places discovered were in very small streams, and it is possible that many others had dried up before we arrived. *S. metallicum*, on the other hand, was easy to find in the pupal stage, easier, on the Mountain Pine Ridge, than the numbers of adults observed there would have led one to expect.

As is usual in the SIMULIIDAE the pupae with a robust type of gill—in this case those of the subgenus *Hemicnetha*—were found in fast water. *S. pulverulentum* was abundant in rapids of the Western Branch of the Belize River, but very few were found in rapids at Guacemallo, and these were on a moss-like species of the Podostemaceae. The pupae of *S. quadrivittatum* and of *S. metallicum*, which were usually found in small streams, have very slender gill filaments.

Blood-sucking.

The numbers of adults collected on man at various times were as follows:

	S. quadrivittatum	*S. samboni?*	*S. veracruzanum*	*S. metallicum*
Mountain Pine Ridge (by day)	66	0	0	0
Stann Creek valley and R. Sibun area (by day)	9	0	1	165
Cool Shade (at dusk)	3	1	0	0

Only two species, *S. quadrivittatum* and *S. metallicum*, were important man-biters at the time of our visit. In two of the few timed catches made we took 43 examples of *S. quadrivittatum* in 30 minutes at Privacion Creek, and 24 of a mixture of the two species in ten minutes at Fairweather Creek. At Middlesex, which has a bad reputation for ' batlas ', we recorded more than 20 flies on a man in a single count.

Seasonal Changes.

We were not long enough in the country to study seasonal changes but it was obvious that the numbers of flies in the Mountain Pine Ridge and at Caves Branch and Sibun were declining early in February with the onset of the dry season, although there were still many at Middlesex. ' Batlas ' are said to die out on the Pine Ridge in the summer.

Summary.

Several collections of pupae and adults of Simuliid Diptera were made in British Honduras between 9th January and 18th February 1958. Samples were collected in the Mountain Pine Ridge and El Cayo areas in the west, and along the highway traversing the eastern part of the country between Caves Branch and Stann Creek.

Thirteen species of *Simulium* were found, nine of which are named, including *S. quadrivittatum* Lw. and *S. metallicum* Bellardi which are very annoying biters. A few observations on distribution and habits are recorded.

Of the two anthropophilic species of *Simulium* found, one is known to be a vector of onchocerciasis, if only of secondary importance, and the capability of the other to transmit the disease is unknown. The disease has apparently never been established in British Honduras and is present in Guatemala. The risk of infection to settlers moving into territory near Guatemala cannot be assessed without detailed knowledge of the epidemiology of the disease in Central America.

Acknowledgements.

We are indebted to Dr. E. Losonczi, formerly Director of Medical Services, British Honduras, for much assistance; to Dr. L. Vargas for sending Mexican specimens of *Simulium* for comparison with ours; and to other helpers mentioned in the general account of our work.

References.

Bradt, S. (1932). Notes on Puerto Rican black flies.—*Puerto Rico J. publ. Hlth* **8** pp. 69–81.

Dalmat, H. T. (1952). Descriptions of two new species of *Simulium* (Diptera, Simuliidae) from Guatemala.—*Ann. ent. Soc. Amer.* **45** pp. 339–347.

Dalmat, H. T. (1955). The black flies (Diptera, Simuliidae) of Guatemala and their role as vectors of onchocerciasis.—*Smithson. misc. Coll.* **125** no. 1, 425 pp.

Dampf, A. (1943). La crisálida de *Eusimulium ochraceum* (Walker, 1860) (Insecta Diptera).—*Rev. Soc. mex. Hist. nat.* **4** pp. 33–41.

Dunn, L. H. (1934). Entomological investigations in the Chiriqui region of Panama.—*Psyche* **41** pp. 166–183.

Fairchild, G. B. (1940). Notes on the Simuliidae of Panama (Dipt., Nematocera).—*Ann. ent. Soc. Amer.* **33** pp. 701–719.

Garnham, P. C. C. & Lewis, D. J. (1959). Parasites of British Honduras with special reference to leishmaniasis.—*Trans. R. Soc. trop. Med. Hyg.* **53** pp. 12–40.

León, L. A. & Wygodzinsky, P. (1953). Los simúlidos del Ecuador (Diptera), su importancia en medicina humana.—*Bol. Inf. cienc. nac.* **6** pp. 269–288.

Lewis, D. J. (1958). The recognition of nulliparous and parous *Anopheles gambiae* by examining the ovarioles.—*Trans. R. Soc. trop. Med. Hyg.* **52** pp. 456–461.

Malloch, J. R. (1914). American black flies or buffalo gnats.—*Tech. Ser. U.S. Bur. Ent.* no. 26, 72 pp.

Ortiz C., I. (1944). *Simulium quadrivittatum* Loew. Su presencia en Venezuela.—*Bol. Lab. Clín. Razetti* **5** pp. 243–246.

Pinto, C. (1932). Simulidae da America Central e do Sul (Diptera).—*7. Reun. Soc. argent. Pat. reg. Norte, Tucumán 1931* pp. 661–763.

Roubaud, E. (1906). Insectes Diptères. Simulies nouvelles ou peu connues.—*Bull. Mus. Hist. nat., Paris* **1906** pp. 517–521.

Surcouf, J. M. R. & Gonsalez-Rincones, R. (1911). Essai sur les Diptères vulnérants de Venezuela. Première partie.—320 pp. Paris, Maloine.

Vargas, L. (1945). Simúlidos del Nuevo Mundo.—*Monogr. Inst. Salubr. Enferm. trop.* no. 1, 241 pp.

Vargas, L. & Díaz Nájera, A. (1951). Nota sobre los simúlidos de México y su distribución geográfica (Diptera: Simuliidae).—*Rev. Inst. Salubr. Enferm. trop.* **12** pp. 89–100.

Vargas, L. & Díaz Nájera, A. (1957). Simúlidos mexicanos.—*Rev. Inst. Salubr. Enferm. trop.* **17** pp. 141–399.

Vargas, L. & Díaz Nájera, A. (1958). Nota sobre *Simulium* (*Psilopelmia*) *bivittatum* Malloch, 1914 (Diptera: Simuliidae).—*Rev. Inst. Salubr. Enferm. trop.* **18** pp. 13–30.

Vargas, L., Martínez Palacios, A. & Díaz Nájera, A. (1946). Simúlidos de México. Datos sobre sistemática y morfologia. Descripción de nuevos subgéneros y especies.—*Rev. Inst. Salubr. Enferm. trop.* **7** pp. 101–192.

© Commonwealth Agricultural Bureaux, 1959.

INSECT INFESTATION ASSOCIATED WITH FRENCH SHELLED WALNUTS WITH PARTICULAR REFERENCE TO THE OCCURRENCE OF *APHOMIA GULARIS* (ZELL.) (LEP., GALLERIIDAE).

By K. G. Smith, B.Sc., F.R.E.S.

Infestation Control Division, Ministry of Agriculture, Fisheries & Food, Rodney Street, Liverpool.

French shelled walnuts shipped from Bordeaux are imported into Britain and from time to time are transhipped to other countries, through the port of Liverpool. Individual shipments may be small but a more or less regular weekly flow is maintained throughout the year. These nuts, which are initially of good quality, frequently arrive infested by insects and mites. Since 1955, many such cargoes passing through Liverpool have been fumigated. The purpose of this paper is to summarise the information obtained from inspections in that port of cargoes arriving between July 1955 and June 1958 and to emphasise the part such traffic may have in the dispersal of *Aphomia gularis* (Zell.), a serious storage pest of nuts, dried fruit and cereals, which has as yet only a limited distribution (Smith, 1956).

Inspection and Interpretation of the Results.

The nuts arrive packed in paper-lined wooden cases in parcels of an average size of 50 cases. Each parcel is stencilled with a distinguishing mark, a quality mark and, usually, the name and address of the packer. Inspection was done on the quay within 24 hours of the discharge of the ship, care being taken to see that no infestation could have occurred between the time of discharge and the inspection.

In practice, all the species of storage pests present could be found, and an assessment of the infestation made, by paying particular attention to the gap between the tongued-and-grooved boards of the cases. Inspection, therefore, took the form of a very thorough search of the outsides of the cases and, with the exception of parcels for transhipment, the opening of a number of each parcel. Levels of infestation were assessed on the standards normally adopted by the Ministry (Freeman, 1948). Where a number of stages of a species occurred, an indication of the period of its life-cycle could be obtained, but the interpretation of the results in terms of seasonal abundance of the species is complicated by considerable fluctuations in the quantity, age and origin of the nuts seen throughout the year. No shipments at all were received during the month of July 1957.

Though cross-infestation of species present as adults or active larvae may have occurred between parcels during the voyage, *A. gularis* was, with few exceptions, found as larvae in diapause which had been spun up for some weeks and could therefore, with some certainty, be traced back to the places of origin in France. The frequent association of such larvae with parcels shipped by certain packers further confirmed their origin.

Origin and Character of Trade.

Except for isolated parcels which had originated from farther afield, the majority of those seen in Liverpool came from towns centred about Sarlat-en-Perigord, in the Dordogne, which was by far the most important packing centre.

All were shipped by way of Bordeaux, arriving in Liverpool after a voyage of about four days.

Seasonal fluctuations in both the quantity of nuts shipped and the number of packers shipping during the season was considerable. Usually the majority of packers only shipped in the autumn following the harvesting of the nuts. At that time relatively large quantities were shipped to Britain and other countries. A small number of packers, however, continued to ship small quantities throughout the spring and summer. In 1955, stocks of the previous season's nuts had apparently been exhausted by the time those of the new crop commenced to be shipped but in 1956–57 a period of six months occurred during which time nuts harvested in the seasons of 1955 and 1956 were being shipped together. A similar overlap of four and a half months occurred between the 1956 and 1957 seasons, shipped during 1957–58.

Insects and Mites collected.

Twenty species of insects were recorded (Table I). Of these only six were found regularly, the remainder occurring sporadically. Of the species found regularly, *Aphomia gularis*, *Plodia interpunctella* (Hb.) and *Oryzaephilus surinamensis* (L.) were frequently numerous. The remainder, *Cryptophagus subfumatus* Kraatz, *Nemapogon granella* (L.) and *Enarmonia* sp. were never so abundant. As only larvae of the latter genus were found a specific identification was not possible.

TABLE I.

Levels of infestation of different insects found on 840 parcels of walnuts (135 cargoes) inspected.

Species	No. of parcels	Very few	Few	Moderate numbers	Fair numbers	No. of cargoes
Oryzaephilus surinamensis (L.)	236	137	62	33	4	84
Cryptophagus subfumatus Kraatz	62	55	7	0	0	46
Dermestes lardarius L. ..	9	9	0	0	0	4
Trogoderma granarium Everts	1	1	0	0	0	1
Tribolium castaneum (Hbst.) ..	16	15	1	0	0	9
Tenebroides mauritanicus (L.)	6	6	0	0	0	7
Enicmus minutus (L.)	2	2	0	0	0	2
Mycetaea hirta (Marsham) ..	1	1	0	0	0	1
Ptinus fur (L.)	1	1	0	0	0	1
Aphomia gularis (Zell.)	104	77	10	15	2	58
Plodia interpunctella (Hb.) ..	76	64	11	1	0	45
Nemapogon granella (L.) ..	34	34	0	0	0	26
Enarmonia sp.	38	38	0	0	0	27
Anagasta kühniella (Zell.) ..	8	8	0	0	0	8
Bracon hebetor Say	1	1	0	0	0	1
Lyctocoris campestris (F.) ..	1	1	0	0	0	1
Lachesilla pedicularia (L.) ..	2	2	0	0	0	2
Myopsocnema annulata (Hagen)	1	1	0	0	0	1
Lepinotus patruelis Pearman ..	1	1	0	0	0	1
Tyrophagus tenuiclavus Zkhv.	1	0	0	1	0	1

A. gularis was the most frequent Lepidopterous species. Diapause-stage larvae were found spun up in cases arriving between July and the following April. Generally the cracks between the boards were used as pupation sites though occasionally holes were bored in the woodwork. On one occasion as many as 20 larvae were found spun up beneath a two-inch flake of a tongued and grooved board. Pupae were found in May and half-grown larvae in June. The only adult found occurred in July but had been dead some time.

Larvae of *P. interpunctella* occurred frequently from July onwards wandering over the cases or spun up in the cracks. In May, June and October, pupae were found and in July, live adults were found inside a case.

Larvae of *Enarmonia* sp., though frequently found between October and the following April, occurred only in ones and twos, spun up in the cracks of cases containing nuts of the current season. It is apparent that they had originated from nuts infested before being harvested.

Larvae of *N. granella* were found frequently in small numbers spun up in the cracks of cases which, from their dirty external appearance, appeared to have been in store some time before use. Pupae were found in February and adults in July and October.

Of all the species found, *O. surinamensis* was the most abundant. Adults occurred on the outsides and on the contents of cases throughout the year. In the winter they were less active and more frequently found clustered between the cracks of cases. On one occasion, 150 were found inside an inch-and-a-half length of tongue and grooving. Larvae were very infrequently found in ones and twos.

As with larvae of *N. granella*, adults of *C. subfumatus* were frequent in ones and twos and were similarly associated with cases of a dirty appearance. Pupae were found in cracks of such cases in May and October and September.

Significance of the Infestation.

An unusual feature of the infestations found has been the undamaged condition of the walnuts. Apparently the nuts had not had time to become seriously attacked by the insects and had probably been cracked and packed immediately prior to shipment. Some cross-infestation may have occurred between despatch and their arrival in Liverpool but the close association of spun-up larvae and quiescent adults with the wooden cases, particularly of those from certain packers, strongly suggests that the cases themselves had become infested before use. Such infestation may have originated from stocks of uncracked, broken or discarded nuts and waste (Bruneteau, 1957). During the period under review there was an apparent change in the composition and level of infestation. It will be seen (fig. 1) that whereas there was a rapid increase in the occurrence of *Oryzaephilus* from 1955 onwards there was a decrease, of a less marked nature, in that of *Aphomia* and *Plodia*. This may have been associated with the carrying over of the previous season's nuts from one year to the next. A not so obvious rise in the frequency of *Nemapogon* and *Cryptophagus* may have been the result of the same conditions. On the other hand the seasonal frequency of *Enarmonia* sp., a field pest, remained unchanged.

To judge the significance of the infestation by the percentage cargoes or tonnage found to carry an infestation (Table II) is misleading, as few cargoes were uniformly infested and the majority of the larger cargoes, which only arrived

TABLE II.

Infestation in terms of a percentage of the cargoes, parcels and tonnage of walnuts inspected during the period July 1955 to June 1958.

	Totals inspected	Percentage clear	Percentage infested
Cargoes ..	135	22	78
Parcels ..	840	47	53
Tonnage ..	1421	77	23

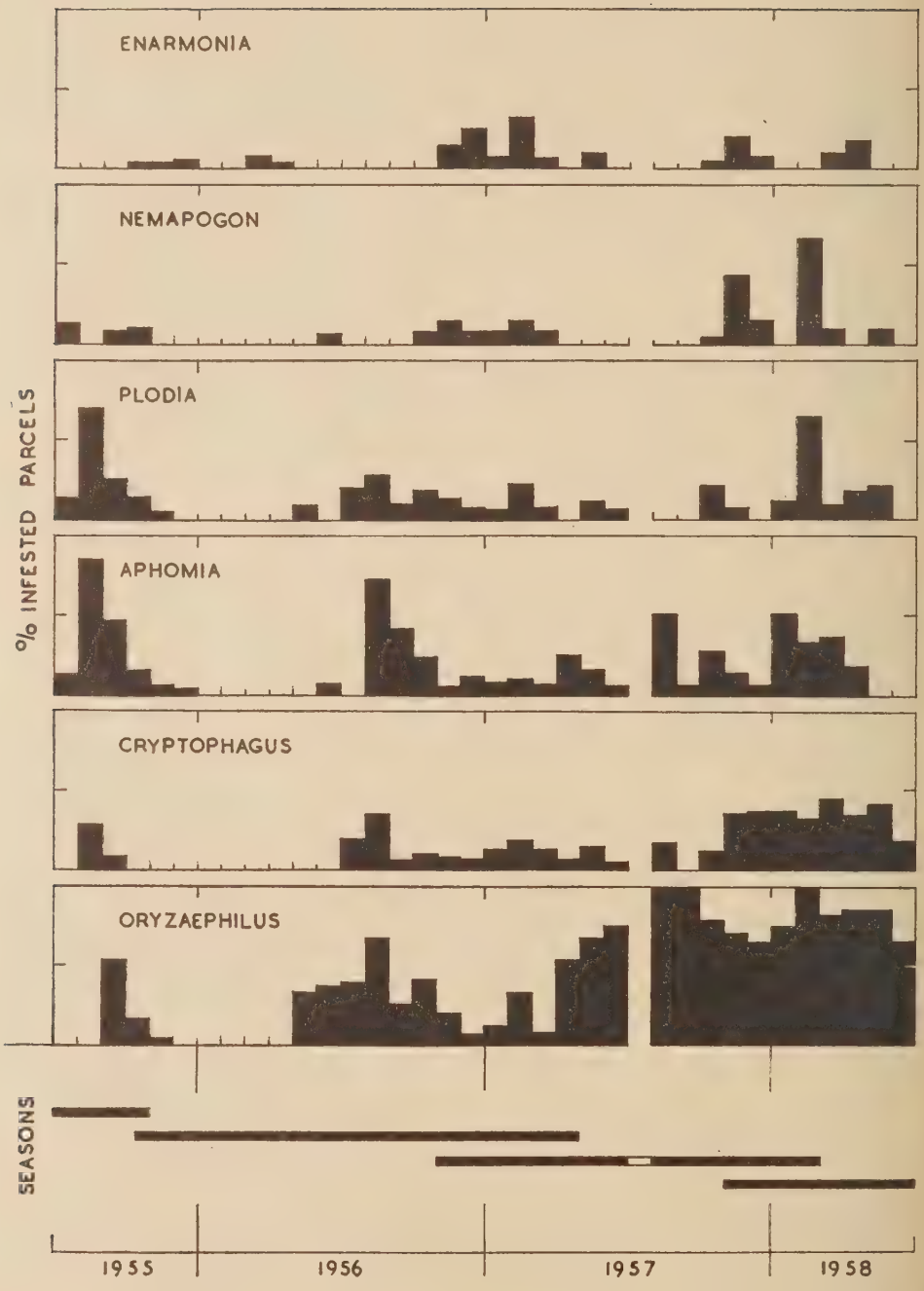


Fig. 1.—Percentage of parcels infested by the major pests, and the periods during which nuts of successive seasons were shipped.

at the beginning of the season, were uninfested. As it is the parcel which is the unit in which the cargoes are distributed, a more accurate picture is presented by the percentage of the parcels found infested. If the figures are broken down into the percentages of 'lightly' and 'moderately' infested parcels inspected during consecutive six-month periods (Table III) it is seen that there was a general increase both in the level of the infestation and the proportion of parcels found to be infested. This increase was associated with the increase in the frequency of *O. surinamensis*.

TABLE III.

Level of general infestation on parcels of walnuts inspected during successive six-month periods.

Period	Total no. parcels	Percentage clear	Percentage lightly infested	Percentage moderately infested
1955 July–December ..	263	81	18	1
1956 January–June ..	187	92	8	0
1956 July –December ..	132	40	57	3
1957 January–June ..	122	45	49	6
1957 July–December ..	83	16	54	30
1958 January–June ..	53	13	62	25

Though several species were frequently imported in these parcels, it might be argued that the average levels of 41 per cent. lightly and 11 per cent. moderately infested were too slight to warrant action. This might be so for some raw materials but not for nuts that are to be used without further processing in the confectionery or retail trades. Whereas some of the species found may not be able to do more than maintain themselves in unheated premises in Britain, all are capable of breeding rapidly in such heated premises as bakeries, biscuit and chocolate factories where walnuts are used. Under such conditions not only may the nuts become considerably damaged and unfit for use but other stock and even finished products may become cross-infested.

Infestations established in premises are often difficult to eradicate and may lead to the need for expensive control measures being applied over many years. Having once established itself in one place, a species may spread to others along the channels of trade. Of the species recorded on the walnuts this particularly applies to *A. gularis*, which is not found generally in Britain and has not yet become established in many other countries where climatic conditions appear favourable for its development. The infrequency of records of interception of this pest has in the past led to the belief that its incidence in the channels of world trade was very low. This survey has, however, shown that its association with the trade of French shelled walnuts may be high. An analysis of the origins of infested parcels shows that it probably occurs throughout the nut producing region and its port of Bordeaux. Judging by the incidence of interception, which was over four times the total of previous known world records, dissemination of the pest in this way would appear to be potentially serious. Cargoes were seen in transit at Liverpool destined for the eastern United States and Canada, the

Republic of Ireland and New Zealand. If further spread of this pest is to be prevented, all such cargoes should be fumigated before shipment. The presence of other species of insects, perhaps equally important pests of walnuts, would also justify fumigation even though they are already widely distributed. During three years, all or part of 58 per cent. of the cargoes received in Liverpool had to be fumigated on arrival. It is thus evident that many nut exporters do not take advantage of the excellent fumigation facilities at Bordeaux and probably do not adopt adequate measures to control the infestations in their premises. A more general application of the control measures advocated by Bruneteau (1957) would probably remedy matters.

Summary.

Walnuts grown and shelled in the Dordogne and adjacent regions of France are exported to Britain and other countries. The inspection of cargoes arriving at Liverpool between July 1955 and July 1958 has shown that they may frequently be infested by a number of species of insect pests. Of the 20 species recorded, six occurred regularly. These were *Oryzaephilus surinamensis* (L.), *Aphomia gularis* (Zell.), *Plodia interpunctella* (Hb.), *Cryptophagus subfumatus* Kraatz, *Nemapogon granella* (L.) and *Enarmonia* sp. During that period, changes occurred in the levels of infestation on parcels and the relative abundance of the species. In particular, there was a considerable increase in the occurrence of *O. surinamensis*. Though the general levels of infestation were light, parts of 58 per cent. of the cargoes had to be fumigated to prevent pests being distributed to factories, bakeries and shops in Britain and on transhipped parcels to Canada, U.S.A. and the Republic of Ireland. Though many of the species found are already established in those countries where conditions are suitable for their development some are still limited in their distribution. These include *A. gularis*, a serious pest of nuts, dried fruit and cereals. If the further spread of this and the other pests is to be prevented there is need for a more general application of control measures in the country of origin with strict control and possibly fumigation of cargoes before shipment.

Acknowledgements.

The work described in this paper was done as part of the work of the Infestation Control Division of the Ministry of Agriculture, Fisheries and Food. The author wishes to express his thanks to Dr. J. A. Freeman for his encouragement and for reading the draft, to Dr. A. Hughes for identifying the mites and Dr. E. Broadhead the Psocoptera, and to Mrs. M. T. Armstrong and Mr. E. T. Bezant for confirming the identification of the other species.

References.

Bruneteau, J. (1957). Les insectes des entrepôts de noix et leur destruction.—*Phytoma* **9** no. 92 pp. 10–14.

Freeman, J. A. (1948). World foci of infestation and principal channels of dissemination to other points, with suggestions for detection and standards of inspection.—*FAO agric. Stud.* no. 2 pp. 15–34. Washington, D.C., Fd Agric. Org., United Nations.

Smith, K. G. (1956). The occurrence and distribution of *Aphomia gularis* (Zell.) (Lep., Galleriidae), a pest of stored products.—*Bull. ent. Res.* **47** pp. 655–667.

THE SUSCEPTIBILITY OF THE RICE PENTATOMID BUG, *SCOTINOPHARA LURIDA* (BURM.), TO INSECTICIDES, AND THE INSECTICIDAL CONTROL OF THIS PEST IN CEYLON.

By H. E. Fernando

Entomologist, Department of Agriculture, Peradeniya, Ceylon.

The general cultural methods of control of the rice Pentatomid bug or black bug of rice, *Scotinophara lurida* (Burm.), in Japan, have been discussed by Katsumata (1929) and by Kawasi (1954). Reported studies on the susceptibility of the rice Pentatomid bug to the action of insecticides and its insecticidal control, however, are few. Benzene hexachloride dusts, parathion dusts and tobacco dusts have recently been recommended in Japan for the control of this pest (Kawada & others, 1954) in the field. Kobayashi & Noguchi (1956) have studied the variation of the susceptibility to parathion of *S. lurida* in its nymphal and adult stages during various seasons of the year and have established a relationship between the stage of development of the adult and susceptibility to parathion.

S. lurida is a very serious pest of the rice crop in certain areas of Ceylon (de Alwis, 1941; Fernando, *in press*).

Two crops of rice are grown each year on which five to six generations of the bug develop. Two of these, which become adult at the time when the particular crop is mature or being harvested, aestivate in the stubbles and do not become sexually mature until later. The generations that become adult earlier in each crop season become sexually mature at once, and mate and oviposit. In 1952, extensive studies were initiated on the susceptibility of this pest to the action of a series of modern organic insecticides and on the insecticidal control of the pest in the field. This paper reports the results of these investigations.

Susceptibility of *S. lurida* to Insecticides.

Material and methods.

Adult bugs, of both sexes, used in these studies were collected from the field during various seasons of the year and while the bugs were in various stages of adult development. In the laboratory the most vigorous specimens were selected and placed in 300 ml. narrow-mouthed conical flasks. Fifty bugs were placed in each flask, which was then provided with a tight plug of cotton-wool moistened with water. Paper strips were suspended from the cotton-wool plug of the flask to the bottom of each flask to provide for free movement of the bugs, which were maintained thus for 24 hours prior to treatment.

The insecticides tested in these studies were DDT, γ BHC, endrin, dieldrin, malathion, Chlorthion, Guthion (O,O-dimethyl S-(4-oxo-benzotriazino-3-methyl) phosphorodithioate), Dipterex (dimethyl 2,2,2-trichloro-1-hydroxyethylphosphonate), diazinon and parathion. The chlorinated hydrocarbon insecticides used were 99 to 100 per cent. pure crystalline products. The organophosphorus insecticides used were in emulsifiable concentrate formulations. All insecticides were dissolved in acetone for application of various dosages in 1 cu. mm. quantities of solution to the surface of the abdomen by way of a micropipette arrangement as described by Trevan (1922). Treated bugs were replaced in the conical flasks and the flasks placed in a chamber maintained at a constant temperature of 30 ± 1°C. and a relative humidity of 92 per cent. The mortality of treated bugs was recorded at 12-hour intervals after treatment. Bugs which

TABLE I.

Susceptibility of adults of *S. lurida* in various stages of development to a series of insecticides.
LD50 after 24 hr.

Insecticide	LD50 for each stage in µg. insecticide per bug			Ratio of LD50's of various stages					
	Freshly emerged (F)	Sexually mature (S)	Aestivating (A)	F/S	F/A	S/F	S/A	A/F	A/S
γ BHC ..	0·00661 S.E. 0·00246	0·00913 S.E. 0·00332	0·0205 S.E. 0·00139	0·7239	0·3224	1·3812	0·4453	3·1013	2·2453
Endrin ..	0·0252 S.E. 0·00235	0·0113 S.E. 0·00132	0·0832 S.E. 0·00214	2·2300	0·3028	0·4484	0·1358	3·3015	7·3628
Dieldrin ..	0·0252 S.E. 0·00158	0·020 S.E. 0·00347	0·214 S.E. 0·00289	1·2600	0·1177	0·7936	0·0934	8·4920	10·7000
DDT	2·52 S.E. 0·00264	0·458 S.E. 0·00458	5·5 S.E. 0·00138	5·5021	0·4581	0·1817	0·0832	2·1825	12·0087
Parathion ..	0·0209 S.E. 0·00224	0·0252 S.E. 0·00355	0·324 S.E. 0·00148	0·8293	0·0645	1·2057	0·0777	15·5023	12·8571
Dipterex ..	0·0178 S.E. 0·00061	0·033 S.E. 0·00468	0·152 S.E. 0·00135	0·5393	0·1171	1·8539	0·2171	8·5393	4·6060
Diazinon ..	0·0258 S.E. 0·00513	0·163 S.E. 0·00174	0·491 S.E. 0·00200	0·1582	0·0525	6·3178	0·3319	19·0310	3·0122
Malathion ..	—	0·364 S.E. 0·00142	—	—	—	—	—	—	—
Guthion ..	—	0·166 S.E. 0·00276	—	—	—	—	—	—	—
Chlorthion ..	—	0·105 S.E. 0·00246	—	—	—	—	—	—	—

F = Freshly emerged
S = Sexually mature bugs
A = Aestivating
S.E. = Standard Error

were knocked down on their backs and were incapable of co-ordinated locomotion when re-orientated were regarded as dead for purposes of mortality counts. At least 100 bugs were used for each dosage of insecticide tested, and for each insecticide four to six dosages were used so as to obtain a wide range of mortality figures for plotting of dosage-mortality curves. The figures used for plotting the curves were those obtained 24 hours after treatment. Values of LD50 were read off from these curves.

Results.

The dosage-mortality curves obtained in these studies are presented in figs. 1, 2 and 3, and the values of LD50 derived from them are shown in Table I. At the stage when bugs were sexually mature, mating and ovipositing, ten insecti-

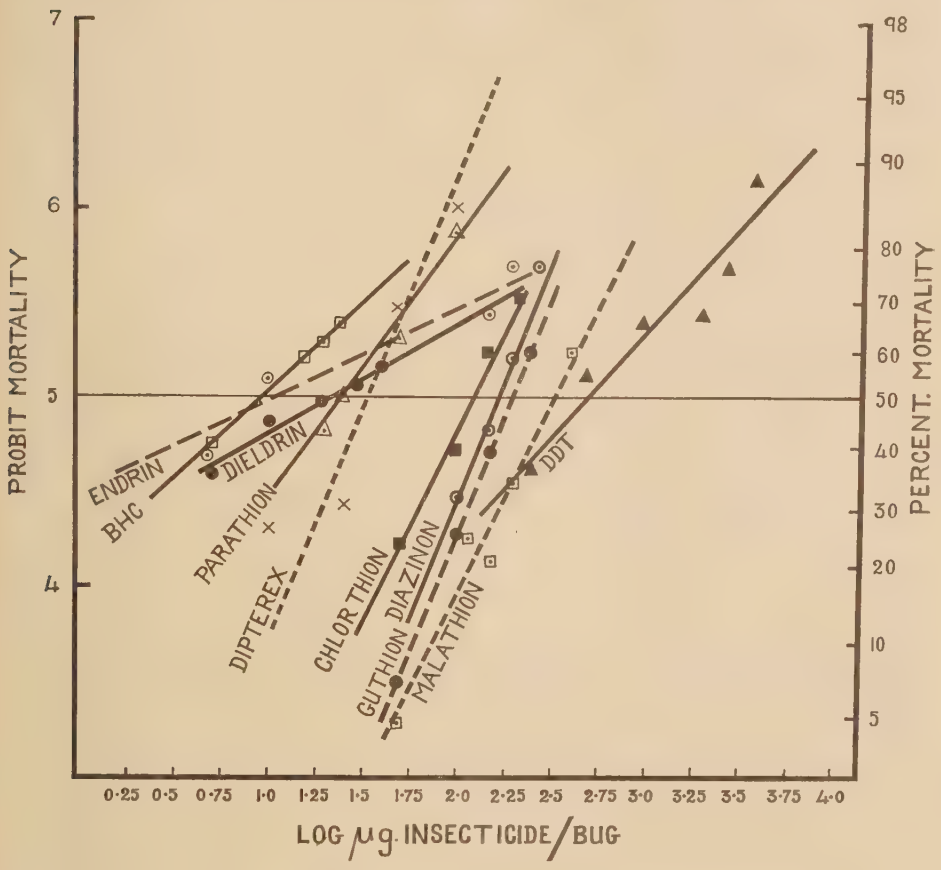


Fig. 1.—Twenty-four-hour dosage-mortality curves for a series of insecticides tested against sexually mature *S. lurida*.

cides were tested and the results are illustrated in fig. 1. On the basis of these curves and the LD50 values obtained, the ten insecticides can be arranged in descending order of toxicity to sexually mature bugs as follows:—γ BHC > endrin > dieldrin > parathion > Dipterex > Chlorthion > diazinon > Guthion

> malathion > DDT. Spraying of tracts is usually carried out at about the time the bugs are sexually mature, and the results in Table I are of special interest because the mortalities of bugs obtained by field spraying of the formulated products do not follow strictly those obtained in laboratory studies where acetone solutions of the insecticides were used.

A comparison of the susceptibility of adults of *S. lurida* in the various stages of adult development, *viz.*, freshly emerged, sexually mature (*i.e.*, mating and oviposting) and aestivating, provided very interesting information. The freshly emerged adult bugs were obtained from the first generation of bugs to develop entirely on the young rice crops in January. These bugs became sexually mature and proceeded to mate and oviposit in February. The condition of sexual development was assessed both by field observations and by dissection in the laboratory. Bugs of a later generation, becoming adult at the time of harvest and representing the aestivation stage, were collected from the aestivation sites such as cracks in the soil, débris in the rice stubbles, etc. (Fernando, *in press*) during the months of March and April when there was no crop or water in the fields. The term 'aestivating' is used here rather loosely to designate what might be either a quiescent or diapause stage of this insect which occurs in between one season

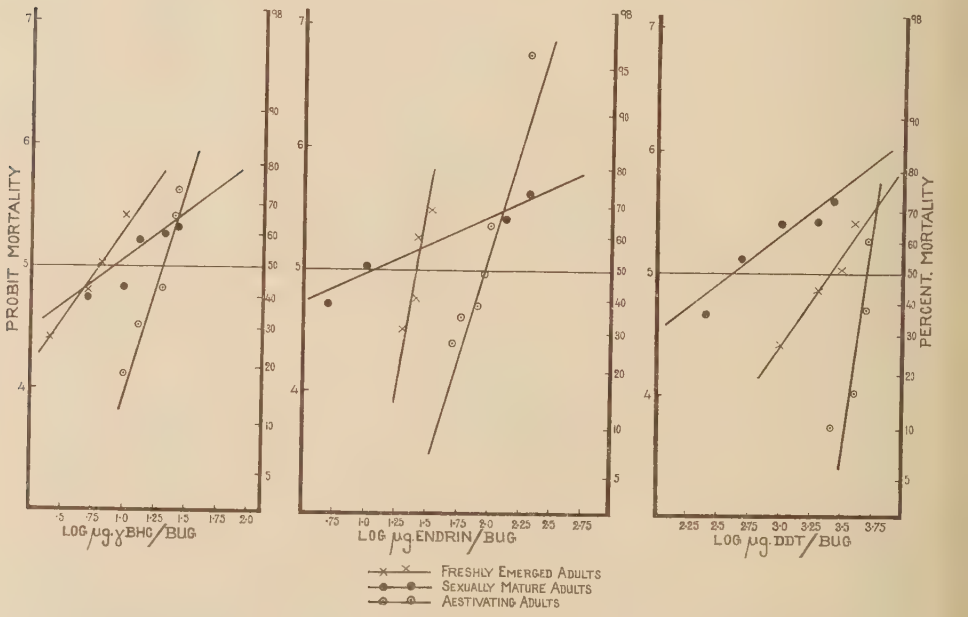


Fig. 2.—Twenty-four-hour dosage-mortality curves for three chlorinated hydrocarbon insecticides tested against *S. lurida* in three stages of adult development.

of rice cultivation and the next. The dosage-mortality curves obtained with these stages are shown in figs. 2 and 3, and numerically the values of LD50 derived from them in Table I.

The data indicate that the aestivating bugs are highly resistant to all the insecticides tested when compared with the freshly emerged and the sexually mature bugs. This fact is of special interest because it was established by dissection that aestivating bugs are all sexually immature. Another interesting

feature is that whereas freshly emerged adults are more susceptible than sexually mature adults to the organophosphorus compounds tested, they are sometimes less susceptible than sexually mature adults to chlorinated hydrocarbon compounds, though equally sensitive to dieldrin and slightly more sensitive to γ BHC (figs. 2 & 3).

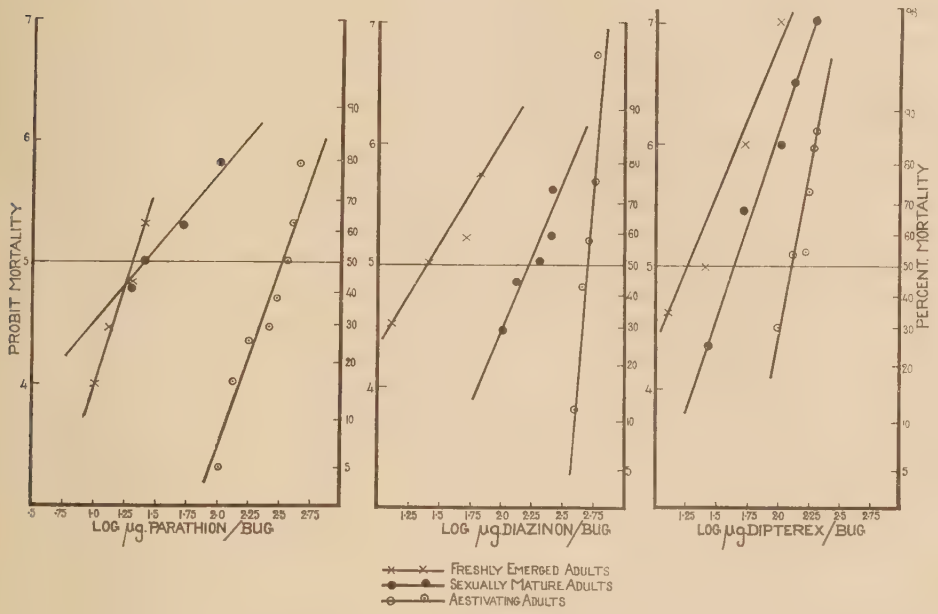


Fig. 3.—Twenty-four-hour dosage-mortality curves for three organophosphorus insecticides tested against *S. lurida* in three stages of adult development.

Field Investigation on the Insecticidal Control of *S. lurida*.

Material and methods.

Rice tracts heavily infested by the pest were selected in the Walawe River Right and Left Bank Colonization Schemes in the Southern Province for field testing of a series of insecticides in the control of the pest. The crop was usually in the seedling stage when the investigations started. Investigations were continued so as to obtain data on the control of the pest by insecticides at all stages of the growth of the crop. Spraying was done with a hand-operated sprayer of the knapsack type, equipped with hollow cone nozzles, while dusting was done with a rotary type hand-operated duster.

In these investigations the insecticides used were predominantly in the emulsifiable concentrate formulation. This was the formulation preferred on account of its good adhesive qualities when applied to the rice plant. On the three-week-old rice seedling crop, spraying was carried out at the rate of 15 to 20 gal. spray fluid per acre. Larger plants, about two months old, required a minimum of 30 gal. of spray fluid per acre for good coverage of the crop and control of the pest. Dusts were used on the maturing crop on account of the difficulty of spraying and the relative inaccessibility of the bugs to sprays at that stage of growth of the crop.

Each insecticidal spray or dust treatment was carried out on a separate area of seedling rice bounded on all sides by bunds. Each such unit of a rice tract, referred to locally as a 'liyadda,' usually covered an area of about 1/10th of an acre but varied considerably; all those chosen for insecticidal treatment were upwards of 1/10th acre. For the purpose of calculating gallonage of spray used and observations of bug populations before and after treatments and of mortalities, an area of 1/10th acre was employed within each test liyadda. Bug populations were assessed on 4-sq.-ft. areas in each test plot before and after treatment. All treatments were replicated at least twice. In earlier experiments it was found that bug populations both within treated and untreated areas fluctuated widely from day to day. Consequently the mortality and survival counts of bugs made 24 hours after treatments, when compared with population counts taken before treatments, showed wide discrepancies. Frequently the populations in check plots and even in some treated plots had increased 12 hours after the first observations. These fluctuations in bug populations under observation are believed to be due to normal crepuscular and nocturnal migration of bugs in the field. Therefore, to avoid errors in assessments of the efficacy of insecticidal treatments arising from this cause, a system of caging 4-sq.-ft. areas within treated and untreated areas was devised for observations on bug populations. Firm wire frames, 2 ft. × 2 ft. × 1·5 ft. high were constructed and covered with muslin. The vertical rods extended downwards for a further 1½ ft. and were driven into the mud in the rice-field and served to keep the cages steady.

Bug populations in several 4-sq.-ft. observation areas in the test plots were assessed immediately before insecticidal treatments were carried out. After the liyadda had been treated, muslin cages were placed over these 4-sq.-ft. observation areas. The cages were removed for 12-hourly observations on the mortality and survival of the bugs and then replaced. Dead bugs were usually found floating. Frequently, however, the total number of bugs observed before treatments in the 4-sq.-ft. areas could not be entirely accounted for by the counts of the dead bugs and those live bugs visible on the plants. Examination of the stems of the rice seedlings below the water surface revealed a number of live bugs in this location. Subsequent studies have shown that this pest frequently migrates below water level along the stems of seedling rice (Fernando, *in press*). Assessment of bug populations before and after spray treatments had, therefore, to be made not only by counting the bugs visible on the stems and the leaves of the rice seedlings but also by exploring the portions of the stems below water level.

Results.

In the first series of trials carried out, emulsifiable concentrate formulations of the insecticides DDT, γ BHC, chlordane, toxaphene, malathion and diazinon were tested against the pest. The infested rice crop selected for the trial was a 3-week-old seedling crop with a minimum of 3 in. of water in the tract. The results of this series of tests are given in Table II.

When the rice crop is in the seedling stage, adults of *S. lurida* are very active at dusk and at night. Many of them take wing at this time and alight on new feeding grounds. It is clear, therefore, that under the conditions of the insecticidal trials, where the bugs were enclosed within cages surrounding the rice plants, the insects were exposed to the sprayed surfaces for much longer periods than they would have been under natural conditions. Mortality counts for exposure periods of up to 24 hours to freshly treated plants are therefore considered the best index for an evaluation of any given treatment.

Toxaphene at a high concentration gave very poor control of the pest even after exposure for 36 hours. Chlordane, DDT, dieldrin, γ BHC, malathion and diazinon gave very effective control of the pest at the concentrations tested. In the case of chlordane and DDT, however, the concentrations necessary to achieve

these results were very high. These two insecticides were consequently not used in the field studies.

In the next series of tests, γ BHC, dieldrin, aldrin, endrin, isodrin, malathion, diazinon and parathion were tested as emulsions at dilutions ranging between 0·01 and 0·06 per cent. active ingredient in the spray fluids. The rice crop was six weeks old and spraying was done at the rate of 25 gal. of spray fluid per acre.

TABLE II.

Mortality of adults of *S. lurida* obtained with a series of insecticides tested in the field.

Insecticide and formulation	Active ingredient in spray (%)	Mortality of bugs (%) after exposure for various periods on treated plants			
		12 hr.	24 hr.	36 hr.	48 hr.
Dieldrin 20% E.C.	0·188	100	—	—	—
	0·125	100	—	—	—
DDT 25% E.C.	1·25	81	87·8	100	—
	0·625	33·9	60·6	78·7	100
Chlordane 75% E.C.	0·469	60	85	100	—
	0·234	33·9	60·6	78·7	100
γ BHC 20% E.C.	0·5	100	—	—	—
	0·25	89	97·4	100	—
Toxaphene 47% E.C.	0·58	15·4	44·8	55·1	—
Malathion 50% E.C.	0·088	68·7	100	—	—
Diazinon 60% E.C.	0·29	100	—	—	—

No mortality was observed in the check plots.

The results of this trial are presented in Table III. It will be noted from this table that at relatively low concentrations all the insecticides tested, with the exception of diazinon, gave over 95 per cent. control of the pest in exposure periods of 36 hours. Within the range of dilutions of the insecticides tested, only four insecticides gave 100 per cent. control of the pest within 24 hours of treatment. These were sprays of parathion at 0·02 per cent., malathion at 0·05 per cent., endrin at 0·04 per cent. and γ BHC at 0·06 per cent. The concentrations found to be effective here are in marked contrast to those obtained in LD50 studies recorded earlier in the paper, where γ BHC is the most toxic of the chemicals against this pest.

The availability of a series of organophosphorus insecticides of relatively low mammalian toxicity like Chlorthion and Dipterex necessitated investigations of their value against the pest for comparison of their efficacy with that of other chemicals having higher mammalian toxicity. The insecticides Dipterex, Guthion, Chlorthion, parathion, malathion, diazinon and dieldrin were tested for control of the pest in the field. The crop was two months old and as the

TABLE III.

Mortality of adults of *S. lurida* obtained with series of insecticides tested in the field.

Insecticide and formulation	Active ingredient in spray (%)	No. of replications	No. of bugs in caged areas before treatment	Number of bugs at intervals after treatment						Mortality of bugs (%) at intervals after treatment		
				12 hr.		24 hr.		36 hr.				
				Dead	Alive	Dead	Alive	Dead	Alive	12 hr.	24 hr.	36 hr.
γ BHC 20% E.C.	0·06	2	83	77	6	83	—	—	—	92·7	100	—
	0·04	2	83	71	12	75	8	—	—	85·5	90·3	92·7
	0·03	2	76	54	22	61	15	—	—	71·05	80·3	—
Endrin 20% E.C.	0·06	2	93	86	7	93	—	—	—	92·4	100	—
	0·04	2	88	72	16	88	—	—	—	87·8	100	—
	0·03	2	79	69	10	77	2	—	—	81·3	97·4	—
Parathion 46·7% E.C.	0·03	2	72	72	—	—	—	—	—	100	—	—
	0·02	2	79	75	4	79	—	—	—	94·9	100	—
	0·01	2	79	45	34	53	26	70	9	56·9	67·0	88·6
Malathion 50% E.C.	0·05	2	76	60	16	76	—	—	—	78·9	100	—
	0·026	2	108	40	68	55	53	60	48	37·0	50·9	55·5
Diazinon 60% E.C.	0·05	2	71	56	15	63	8	65	6	78·8	88·7	91·5
	0·025	2	89	42	47	52	37	55	34	47·1	58·4	61·8
Dieldrin 20% E.C.	0·06	3	140	97	43	114	26	140	—	69·2	81·4	100
	0·04	2	78	40	38	60	18	66	12	51·2	76·9	84·6
Isodrin 20% E.C.	0·06	3	186	91	45	122	14	131	5	66·9	89·7	96·3
	0·04	2	76	40	36	52	24	61	15	52·6	68·4	80·2
Aldrin 20% E.C.	0·06	3	133	88	45	121	12	133	—	66·1	90·8	100

TABLE IV.

Mortality of adults of *S. lurida* in field control test.

Insecticide	Active ingredient in spray (%)	Number of bugs in caged areas before treatment	Number of bugs at intervals after treatment				Mortality of bugs (%) at intervals after treatment	
			12 hr.		24 hr.		12 hr.	24 hr.
			Dead	Alive	Dead	Alive		
Dipterex 50% E.C.	0·0312	100	82	18	90	10	82	90
	0·0416	100	100	—	—	—	100	—
	0·0625	100	100	—	—	—	100	—
Chlorthion 50% E.C.	0·0312	100	80	20	96	4	80	96
	0·0416	100	94	6	95	5	94	95
	0·0625	100	100	—	—	—	100	—
Diazinon 60% E.C.	0·0375	100	66	34	69	31	66	69
	0·05	100	74	26	84	16	74	89
	0·075	100	99	1	100	—	99	100
Guthion 20% E.C.	0·0166	100	61	39	69	31	61	69
	0·025	100	84	16	86	14	84	86
Malathion 50% E.C.	0·0416	100	83	17	88	12	83	88
	0·0625	100	98	2	100	—	98	100
Dieldrin 20% E.C.	0·0312	100	62	38	79	21	62	79
	0·0625	100	97	3	100	—	97	100

Spray applied at 30 gal. per acre on 2-month-old crop; two replicates per treatment.
No mortality was observed in the check plots.

infestation was relatively low, adult bugs were introduced into the 4-sq.-ft. observation areas to bring the population to 50 in each of these areas immediately before treatment and caging which followed soon after. Bugs are extremely sluggish in the daytime and normally do not take to the wing. Consequently bugs placed on plants or dropped into the water within about three inches of the edges of the 4-sq.-ft. areas did not move out of these areas before spraying and caging. Spraying was at 30 gal. per acre.

Considering the data on Tables III and IV the 12-hour mortality figures show that the organophosphorus insecticides parathion, Dipterex and very likely Guthion too (although this insecticide could not be tested at higher concentrations than 0·025 per cent. active ingredient) gave the best control of the pest. These insecticides gave 90–100 per cent. mortality of the pest within twelve hours of treatment when applied at concentrations ranging between 0·03 per cent. and 0·04 per cent. When the 24-hour mortality figures are considered, however, it will be noted that the insecticides, endrin especially, and parathion and Chlorthion to a lesser extent, gave 90–100 per cent. mortality of the pest at considerably lower concentrations than required to give the same mortality results in twelve hours after treatment.

In the first series of investigations with insecticidal dusts conducted against bug infestations on a maturing rice crop, γ BHC, aldrin and dieldrin dusts were applied with a rotary hand-duster at the rate of about 30 lb. per acre on areas of 1/10th acre. The treatments were replicated twice. The results of these dusting trials are given in Table V. Dusting was commenced in the morning at about 0630 hr. and was concluded by 0830 hr. There was a heavy dew on the plants and no wind in the tracts at the time of dusting. The results of the trials showed that the dust containing 1·3 per cent. γ BHC was very effective against the pest, giving 100 per cent. control in twelve hours. Dieldrin at 2·5 per cent. active ingredient was less effective but gave the same results in 24 hours. Aldrin dust at 2 per cent. active ingredient was the least effective. For treatment of the

TABLE V.

Action of insecticidal dusts against adults of *S. lurida* in the field.

Conditions before dusting	Insecticide	Active ingredient (%)	Mortality of bugs (%) at intervals after treatment	
			12 hr.	24 hr.
First Trial Plants covered with heavy dew; no wind	γ BHC	1·3	100	—
	Aldrin	2	45·2	71·2
	Dieldrin	2·5	47·8	100
Second Trial Plants dry; strong wind	γ BHC	·65	38	63
	γ BHC	1·3	34	81
	γ BHC	3	49	87
	Aldrin	2	21	38
	Dieldrin	2·5	34	56

Dust applied at 20–30 lb. per acre under varying conditions of weather; two replicates per treatment.
No mortality was observed in the check plots.

maturing crop against bug infestations, therefore, dusting seemed to give very good results, but it was important to evaluate the efficacy of dusting under slightly different conditions.

A second test was carried out with the same insecticides but using dusts containing 0·65 and 3 per cent. γ BHC in addition to those used earlier. In this trial, dustings were carried out against bug infestations, on a crop 2½ months old, under dry, windy conditions in the evening about 1700 hr. The results obtained in this trial, also presented in Table V, differ considerably from those achieved with similar insecticidal formulations in the earlier dusting trials where the plants were moist and there was no wind. However, it is clear from these results that the dusts containing 1·5 and 3 per cent. γ BHC give satisfactory control of infestation of this pest, even under conditions adverse for dusting.

Residual Effectiveness of Insecticides against *S. lurida* under Laboratory and Field Conditions.

Material and methods.

The first series of tests on the residual effectiveness of insecticides against adults of *S. lurida* was conducted under well-regulated laboratory conditions. The rice plants used in the tests were 2½ months old and had good leaf growth. They were growing in pots 4 in. tall and 3½ in. in diameter, four plants to each pot. The pots were drained of water 24 hours before the treatments and watering avoided until after treatments were completed.

The insecticides used in these tests were dieldrin, endrin, parathion, Metasystox and Ekatin. All test insecticides were in the emulsifiable concentrate formulation. Emulsions of the insecticides to be tested were prepared in a 4-gal. bucket. The leaves of the test plants were dipped in the insecticidal emulsions by holding the pots in an inverted position and immersing the leaves in the insecticidal fluid. The test pots were then maintained in an inverted position for about two hours until the leaves were completely dry. The pots were then replaced in their normal upright position and three leaves of plants from each pot enclosed in glass tubing, 3 in. long and 1 in. in diameter. These sections of glass tubing were maintained in a vertical position by attaching them with strips of Sellotape to straight pieces of wire, of 1/8 in. diameter, inserted vertically in the soil of each pot. The leaves were disposed centrally within the glass tubes by closing the open ends of each tube with cotton-wool plugs which encircled the leaves without damaging them. The test was conducted in a room fully aerated and illuminated on all sides by diffused light. Twenty-four hours after the leaves of the test plants had been treated, five adult bugs collected from the field were introduced into each tube to feed upon the enclosed leaves. Each treatment was replicated twice. Mortality counts of the bugs were made 24 hours after the introduction of the insects. The dead or surviving insects were then removed and fresh sets of insects introduced into the tubes. This was repeated every 24 hours until no mortality of bugs was observed in a particular treatment. Every three days, new leaves were selected for infestation with bugs, because leaves that had been exposed to bugs for periods longer than this bore extensive feeding lesions and did not provide adequate feeding sites for the further freshly introduced bugs.

In the second series the residual effectiveness of the insecticides was tested under typical field conditions. Rice plants, 2½ months old, growing in pots under conditions similar to those used in the last series of tests were placed in the field and exposed to sun and rain. In this trial no effort was made to prevent the insecticides from running down the stem and into the soil of the pots. The insecticides were applied as sprays, using a knapsack-type sprayer. Spraying was done at the same rate as would have been done in the field, *viz.*, at about 30 gal. of spray per acre. After the spray treatment the procedure followed for

TABLE VI.

Mortality of adults of *S. lurida* (%) exposed at intervals after treatment of plants.

Conditions of tests	Insecticide and formulation	Active ingredient in dip or spray (%)	Mortality of bugs (%) exposed for 24 hr. on treated plants at daily intervals												
			1 day	2 days	3 days	4 days	5 days	6 days	7 days	8 days	9 days	10 days	11 days	12 days	13 days
Laboratory conditions	Dieldrin 20% E.C.	0·0416	100	86·6	93·3	93·3	86·6	93·3	46·6	80	26·6	13·6	20	33·3	6·6
		0·0625	100	100	86·6	86·6	80	93·3	80	86·6	33·3	20	20	13·6	6·6
		0·125	100	100	100	100	93·3	100	80	86·6	46·6	26·6	33·3	33·3	26·6
	Parathion 46·7% E.C.	0·0194	93·3	46·6	20	6·6	6·6	13·6	0	0	6·6	0	0	0	0
		0·0291	100	80	73·3	20	13·6	20	6·6	6·6	6·6	0	0	0	0
		0·0583	100	100	86·6	53·3	73·5	73·5	33·3	13·6	20	0	0	0	0
	Endrin 20% E.C.	0·0416	100	46·6	26·6	0	20	6·6	0	0	0	6·6	0	0	0
		0·0625	73·3	73·3	33·3	13·6	6·6	13·6	6·6	6·6	0	6·6	0	0	0
		0·125	93·3	73·3	53·3	13·6	6·6	26·6	13·6	6·6	0	0	0	0	0
	Metasystox 50% E.C.	0·02	0	6·6	0	0	0	0	0	0	0	0	0	0	0
		0·05	20	13·6	6·6	0	0	0	0	0	0	0	0	0	0
		0·1	26·6	20	26·6	0	0	0	6·6	0	0	0	0	0	0
	Ekatin 20% E.C.	0·008	0	0	6·6	0	0	0	0	0	0	0	0	0	0
		0·02	13·6	0	6·6	0	0	0	0	0	0	0	0	0	0
		0·01	20	6·6	6·6	0	0	6·6	0	0	0	0	0	0	0

Typical field conditions	Dieldrin 20% E.C.	0·0416	40	13·3	20	13·3	6·6	0	0	0	0	0	0
		0·0625	66·6	13·3	6·6	33·3	6·6	13·3	0	0	0	0	0
		0·125	86·6	60	20	40	20	13·3	6·6	6·6	0	0	0
	Parathion 46·7% E.C.	0·0194	73·3	6·6	6·6	0	0	0	0	0	0	0	0
		0·0291	93·3	20	13·3	6·6	0	0	0	0	0	0	0
		0·0583	100	86·6	33·3	0	13·3	13·3	6·6	0	6·6	0	0
	Endrin 20% E.C.	0·0416	26·6	26·6	13·3	0	0	0	0	0	0	0	0
		0·0625	33·3	26·6	20·0	6·6	0	0	0	0	0	0	0
		0·125	40·6	26·6	33·3	20·0	13·3	6·6	0	0	0	0	0
	Metasystox 50% E.C.	0·02	20·0	6·6	6·6	0	0	0	0	0	0	0	0
		0·05	20·0	20·0	6·6	6·6	0	0	0	0	0	0	0
		0·1	40·0	26·6	26·6	13·3	0	0	0	0	0	0	0
	Ekatin 20% E.C.	0·008	40·6	26·6	13·3	0	0	0	0	0	0	0	0
		0·02	53·3	33·3	20·0	0	0	0	0	0	0	0	0
		0·1	46·6	26·6	33·3	13·3	0	0	0	0	0	0	0

assessing the mortality of bugs exposed to the residues of the various test insecticides on the leaves and described for the last series of tests, was employed. Each treatment was replicated twice.

Results.

The results of these studies are presented in Table VI. Under laboratory conditions the systemic insecticides Ekatin and Metasystox are clearly of no value residually for the control of this pest. Of the others, dieldrin clearly had more prolonged residual effects than endrin and parathion when used both at equivalent and at practical concentrations for field use.

In later trials conducted under field conditions, where the plants were exposed to normal sunlight, the systemic insecticides Ekatin and Metasystox gave better initial kill and their residual effectiveness lasted somewhat longer than when applied under laboratory conditions. The other insecticides, dieldrin, parathion and endrin, however, gave somewhat poorer initial kills and a shorter residual action than when tested under laboratory conditions. Even under field conditions, however, parathion and dieldrin performed better as residual insecticides than the two systemic insecticides tested.

TABLE VII.

Mortality of adults of *S. lurida* (%) exposed at intervals after treatment of plants.

Age of rice plants used	Insecticide and formulation	Method of treatment of plants	Active ingredient in fluid (%)	Mortality of bugs (%) exposed for 24 hr. on treated plants at daily intervals					
				24 hr.	48 hr.	72 hr.	96 hr.	120 hr.	144 hr.
3 weeks	Metasystox 50% E.C.	Painting of leaves	0·1	53·3	33·3	13·3	6·6	0	0
			0·05	20	13·3	13·3	0	0	0
			0·02	13·3	6·6	0	0	0	0
	Ekatin 20% E.C.	Painting of leaves	0·04	46·6	20	13·3	0	0	0
			0·02	33·3	6·6	6·6	0	0	0
			0·008	6·6	6·6	0	0	0	0
	Metasystox 50% E.C.	Application at roots	0·02	100	86·6	73·3	33·3	6·6	0
	Ekatin 20% E.C.		0·008	73·3	33·3	33·3	13·3	6·6	0
10 weeks	Metasystox 50% E.C.	Painting of leaves	0·1	20	13·3	6·6	0	0	0
			0·05	6·6	6·6	0	0	0	0
			0·02	0	0	0	0	0	0
	Ekatin 20% E.C.	Painting of leaves	0·04	13·3	6·6	6·6	0	0	0
			0·02	13·3	0	0	0	0	0
			0·008	6·6	0	0	0	0	0
	Metasystox 50% E.C.	Application at roots	0·02	26·6	53·3	26·6	20	6·6	0
	Ekatin 20% E.C.		0·008	80	80	46·6	26·6	26·6	13·3

Action of Systemic Insecticides against Adults of *S. lurida*.

Material and methods.

The rice plants used in these tests were either 3-week-old seedlings or maturing plants, ten weeks old. These were growing in cement pots, 8 in. square, at the rate of eight plants to a pot. The pots had their water outlets plugged and about ¾ in. of water always covered the surface of the soil in them. The systemic insecticides used in these tests were Ekatin and Metasystox as emulsifiable concentrates. The insecticidal concentrates were diluted with water and were either (a) painted with a camel-hair brush on both sides of all the leaves, special attention being given to preventing the insecticide running down the stems of the plants, or (b) poured into the soil of each pot at the rate of 250 cc. per pot. After application by the two methods had been completed and the leaves of the treated plants in the first one had dried completely, five adult bugs, which had been starved for the preceding 24 hours, were caged on the stem of each of three treated plants. The glass tubes and cotton-wool plugs enclosing the bugs around the test plants were so located as to prevent the bugs from feeding at the basal 1½ in. of the plants or on any of the leaves. The mortalities of the introduced bugs were noted at the end of 24 hours, both living and dead bugs were removed and a new set of starved bugs introduced as before. This procedure was repeated daily until no mortality was observed in the test insects.

Results.

The results of these studies are presented in Table VII. Applied as foliar treatments, both insecticides were relatively ineffective in systemic action against feeding bugs even though used at high concentrations.

The systemic action of Metasystox and Ekatin when used as foliar sprays was markedly lesser on ten-week-old rice plants than on three-week-old rice plants. Applied as a soil treatment, on the other hand, Ekatin was superior to Metasystox and more effective on older plants than on seedlings. Metasystox was more effective as a soil treatment on seedlings than on older rice plants. The dosage rates used, however, are too high for economic application in the field.

Discussion.

The investigations carried out have provided valuable information both from a physiological standpoint and the standpoint of control of the pest in the field. From a physiological standpoint the differences in the value of LD50 for freshly emerged, sexually mature and aestivating bugs and the marked resistance of aestivating bugs to insecticides are points of notable interest.

S. lurida has been shown by Kobayashi & Noguchi (1956), in one generation again, to show progressively increasing tolerance to parathion with advancing maturity of the adult until maximum tolerance to this insecticide is reached at the hibernation stage. In Ceylon, however, *S. lurida* behaves somewhat differently in its response to the action of insecticides. In the case of the active phases of the adult of *S. lurida* tolerance to insecticides does not necessarily increase with increasing sexual maturity of the adult bug in the case of every insecticide. Generally with the chlorinated hydrocarbon insecticides tested, except γ BHC, with increasing sexual maturity the bugs became more susceptible whereas with the organophosphorus insecticides with increasing sexual maturity the bugs became increasingly resistant to the insecticides.

The marked relative resistance of aestivating bugs to all the insecticides studied is a finding similar to that observed by Kobayashi & Noguchi (1956) with parathion in the case of hibernating examples of *S. lurida* in Japan. This resistance to insecticides shown by hibernating bugs in Ceylon ranges from two-fold to nineteen-fold that of active adult bugs. This feature when considered together with the facts that all aestivating bugs are sexually immature and that they show

an entirely different behaviour pattern from that of active adult bugs (Fernando, *in press*), suggests a clear-cut physiological condition in aestivating bugs in Ceylon. Whether this condition is related to a simple quiescence or a more complex diapause can only be elucidated by future study.

The relatively high resistance of aestivating adults of *S. lurida* to insecticides, and the enormous practical problems involved in implementing a chemical control programme against bugs in their aestivating sites, confirms the futility of any effort to control the pest at that stage. On the other hand, the adult bug is more susceptible and accessible to insecticidal treatments during its active stages. During the early stages of the rice crop, spraying has been found to be very effective in the control of the pest but on the maturing crop the pest is only accessible to insecticidal dusts as at this stage the bug restricts its movements, in the main, to the basal regions of the rice plants and the débris surrounding them.

Adults of *S. lurida* on the seedling crop show marked crepuscular and nocturnal activity during which they seek out new feeding grounds. Under the caged conditions obtaining in the experimental plots this activity is prevented and consequently bugs are exposed to the sprayed plant surfaces for unnaturally long periods. A 24-hour period has therefore been regarded as about the maximum that any bug would remain on a sprayed group of plants before migration to an unsprayed area. The 24-hour mortality figures have accordingly been taken as the best index of the applied value of any treatment.

In the field experiments that have been conducted, the chlorinated hydrocarbon insecticides, DDT, toxaphene, chlordane, aldrin, dieldrin, endrin, isodrin and BHC and the organophosphorus insecticides malathion, diazinon, Dipterex, Chlorthion, Guthion and parathion have been tested as emulsion sprays against *S. lurida* on the rice crop. All spray applications were made at the rate of 15 to 30 gallons of spray fluid per acre depending upon the growth and age of the rice crop. Of the insecticides tested, toxaphene, chlordane and DDT gave the poorest control of the pest with only about 85 per cent. mortality in 24 hours when applied at and above concentrations of 0·45 per cent. active ingredient. Parathion was the most effective of the insecticides tested as it gave 100 per cent. control of the pest within 24 hours when applied at a concentration of 0·02 per cent. active ingredient. Chlorthion, Dipterex and endrin and possibly Guthion also (although this insecticide was not tested at a corresponding concentration) were about of equal effectiveness, giving 95–100 per cent. control of the pest within 24 hours when applied at concentrations of 0·03–0·04 per cent. active ingredient. Dieldrin, γ BHC and malathion were nearly equal in their effectiveness in controlling *S. lurida* giving 100 per cent. mortality of the pest in 24 hours when applied at a concentration of 0·06 per cent. active ingredient, while diazinon was somewhat less effective as it gave similar results when applied at a concentration of 0·07 per cent. active ingredient. Aldrin and isodrin were of about equal effectiveness, giving approximately 90 per cent. control when applied at a concentration of 0·06 per cent. active ingredient.

All parathion preparations involve hazards to users under local conditions, while endrin, dieldrin and Guthion have relatively high mammalian toxicities. Endrin, furthermore, has a particularly devastating effect upon all fresh-water fauna, and also upon such other useful animals as the giant lizards (*Varanus* species) and the egrets (*Egretta* species) should they feed upon endrin-poisoned fish, frogs and insects in sprayed rice tracts. Chlorthion and γ BHC emulsions are relatively expensive locally. Dipterex and malathion, on the other hand, are not only very cheap and effective in the control of this pest but also are of low mammalian toxicity and therefore especially safe for use under local conditions. These two insecticides are hence to be favoured for use in the control of *S. lurida* in Ceylon.

The residual effectiveness of the insecticides dieldrin, endrin, parathion, Ekatin and Metasystox in the control of *S. lurida* on the rice plant has been studied. This aspect of the investigation was considered important on account of the nocturnal migrations of the pest during the seedling stage of the rice crop. At what was considered practical concentrations for field application, parathion and dieldrin (at concentrations of 0·05 and 0·125 per cent. active ingredient, respectively) gave the best residual action, with parathion giving the higher initial kill during the first two days after treatment of the plants. For practical purposes therefore a two-day period must be regarded as the limit of effective residual action of parathion and dieldrin and spraying must necessarily be repeated if reinfestation by the pest takes place two days or more after spraying with these two insecticides.

The two systemic insecticides Ekatin and Metasystox showed better residual performance when tested under field conditions than when tested under laboratory conditions. The reverse was found to be true for parathion, dieldrin and endrin. These facts are consistent with the finding that light and temperature are very important factors in the translocation of systemic insecticides as demonstrated by Thomas & Bennett (1954). Both these factors were clearly of a higher order under field conditions than under the laboratory conditions under which the experiments were conducted.

Studies with the two systemic insecticides Metasystox and Ekatin have demonstrated their systemic activity in the rice plants against *S. lurida*. As foliar treatments the two insecticides showed greater systemic action on 3-week-old rice plants than on 10-week-old rice plants. In both cases, however, the foliar treatments gave poor control of the pest. At the later application tested as root treatments both insecticides gave over 70 per cent. control of the pest. On older plants the performance of Ekatin was better than on rice seedlings and markedly superior to that of Metasystox, which proved less effective on older plants than on younger plants. However, the low order of effectiveness of Ekatin and Metasystox as foliar sprays and the very high rate of application of these products required to give control of *S. lurida* when applied as root treatments render these two systemic insecticides of no practical value in the control of this pest.

Summary.

The Pentatomid bug, *Scotinophara lurida* (Burm.), is a serious pest of the rice crop in certain areas of Ceylon. Five or six generations develop on the two annual rice crops, and that which attains the adult stage at the time of harvest of either crop ' aestivates ' and does not become sexually mature until later. The generations that become adult earlier in each crop season become sexually mature forthwith, and mate and oviposit.

In 1952, laboratory experiments to ascertain the susceptibility of adults of *S. lurida* to a range of modern organic insecticides, and field experiments on insecticidal control, were initiated. The insecticides tested were DDT, BHC, endrin, dieldrin, malathion, Chlorthion, Guthion, Dipterex, diazinon and parathion.

In the laboratory, freshly emerged, sexually mature and aestivating bugs were tested separately by topical application on the abdomen, and it was found that the insecticides could be arranged in the following descending order of toxicity, based on the LD50, against the sexually mature adult:— γ BHC, endrin, dieldrin, parathion, Dipterex, Chlorthion, diazinon, Guthion, malathion, DDT. The adults of the aestivating generations, at least prior to becoming sexually mature, were markedly more resistant to all the insecticides tested than were sexually mature bugs of uninterrupted development, the resistance ranging from two-fold to nineteen-fold that of the latter.

There is some indication that tolerance to every insecticide does not necessarily

increase with increasing age and sexual maturity of the normal adult bug. Thus, whereas with the organophosphorus insecticides increasing sexual maturity is associated with an increase in tolerance, with DDT and endrin the bugs appear to become more susceptible with increasing sexual maturity, while with γ BHC and dieldrin there is little change.

The chlorinated hydrocarbon insecticides DDT, toxaphene, chlordane, aldrin, dieldrin, endrin, isodrin and γ BHC and the organophosphorus insecticides malathion, diazinon, Dipterex, Chlorthion, Guthion and parathion have been tested as emulsion sprays against *S. lurida* in the field. DDT and toxaphene gave the poorest results with about 85 per cent. control of the pest in 24 hours when applied at and above a concentration of 0·045 per cent. active ingredient. The other insecticides are arranged thus in descending order of efficacy against the pest considering the minimum dosage required to give 100 per cent. or near 100 per cent. control within 24 hours of application of the treatment:— parathion 0·02 per cent. → endrin 0·03 per cent. = Chlorthion 0·03 per cent. → Dipterex 0·03–0·04 per cent. = Guthion 0·02 per cent. → dieldrin 0·06 per cent. = malathion 0·06 per cent. = γ BHC 0·06 per cent. → diazinon 0·07 per cent. Aldrin and isodrin were of about equal effectiveness giving about 90 per cent. control of the pest within 24 hours when applied at a concentration of 0·06 per cent. active ingredient.

Of the dusts tested, both γ BHC at 1·3 per cent. and dieldrin at 2·5 per cent. gave 100 per cent. control of the pest in 24 hours when applied under still and dewy conditions obtaining in the morning. Under dry, windy conditions however, γ BHC at 1·3 per cent. and 3 per cent. gave better control of the pest than did dieldrin or aldrin dusts.

Parathion, dieldrin, endrin, Metasystox and Ekatin were tested for residual action against *S. lurida* on the rice crop. Parathion was the most effective residually for a period of two days with dieldrin coming next in order of residual effectiveness.

Metasystox and Ekatin were tested for their systemic action against *S. lurida* on three-week-old and ten-week-old rice plants as foliar sprays and as root treatments. Systemic action of a low order of effectiveness against the pest was demonstrated in all cases but the poor results achieved and the high rates of application involved did not warrant their consideration for practical field use.

Acknowledgements.

The author expresses his thanks to Mr. P. Manikavasagar, Assistant in Entomology, Division of Entomology, Department of Agriculture, Ceylon, for his assistance in the conduct of the routine laboratory and field tests during the entire course of this investigation. The author also thanks Mr. Y. Elikawale, Assistant in Entomology, and Mr. M. B. Abeykoon, Laboratory Assistant, both of the Division of Entomology, for their assistance in some of the investigations dealt with in this paper. The author also acknowledges with thanks the assistance and advice of Mr. P. Kanapathipillai, Statistician, Department of Agriculture, Ceylon, on the statistical aspects of this paper.

References.

de Alwis, E. (1941). The paddy Pentatomid bug *Scotinophara* (*Podops*) *lurida* Burm.—*Trop. Agriculturist* **96** pp. 217–220.

Katsumata, K. (1929). Studies on the rice black bug *S. lurida*.—*Ishikawa Pref. agric. Exp. Sta. Rep. 1929.*

KAWADA, A., KATO, S., MUKOO, H. & FUKUNAGA, K. (1954). Insects and diseases of rice plants in Japan.—Nat. Inst. agric. Sci., Tokyo.

KAWASI, E. (1954). Research items on Pentatomid bug, *Scotinophara lurida* Burm.—*Ishikawa Pref. agric. Exp. Sta. Rep. 1954.*

KOBAYASHI, T. & NOGUCHI, Y. (1956). Studies on the control method of the black rice bug, *Scotinophara lurida* Burmeister. I. On the resistance of the black rice bug to ethyl-parathion. [*In Japanese with English summary.*]—*Oyo-Kontyu* **12** pp. 82–86.

THOMAS, W. D. E. & BENNETT, S. H. (1954). The absorption, translocation and breakdown of Schradan applied to leaves, using ^{32}P-labelled material. III. Translocation and breakdown.—*Ann. appl. Biol.* **41** pp. 501–519.

TREVAN, J. W. (1922). An apparatus for measuring small quantities of fluids.—*Lancet* **202** pt. 1 p. 786.

© Commonwealth Agricultural Bureaux, 1959.

PARASITES OF *ANCYLOSTOMIA STERCOREA* (ZELL.), (PYRALIDAE, LEPIDOPTERA) A POD BORER ATTACKING PIGEON PEA IN TRINIDAD.

By Fred D. Bennett

Commonwealth Institute of Biological Control, Trinidad, W.I.

From January 1952 to March 1954, several insects attacking pigeon pea, *Cajanus cajan*, were studied in Trinidad. The only serious Lepidopterous pod borer reared during this period was *Ancylostomia stercorea* (Zell.) (Pyralidae, Phycitinae). The following study was undertaken in conjunction with the rearing and shipment of parasites of *A. stercorea* to Mauritius for trial against *Etiella zinckenella* (Treitschke) and *Maruca testulalis* (Geyer), two Pyralids with somewhat similar habits on the same crop.

Biology of *Ancylostomia stercorea.*

Druce (1896) lists the following synonymy: *Myelois stercorea* Zell.; *Ancylostomia stercorea* (Zell.); *Anerastia ignobilis* Butl.; and *Pempelia diffissella* Zell. The distribution of the species, as summarised by Heinrich (1956) ranges from Florida southward through Mexico, Guatemala, Costa Rica, Panama, Colombia, French Guiana and Brazil as well as throughout many of the West Indian islands. W. J. Hall (*in litt.*) states that material from Nova Scotia, Canada, is present in the British Museum (Natural History) although the record appears to be outside the normal range of the insect. Distribution records additional to those listed by Heinrich, found during this investigation, were British Guiana, Dominica, Montserrat and Antigua.

Heinrich (1956) lists the pigeon pea (*Cajanus cajan*) as the commonest host-plant but also records specimens collected as larvae from chick pea (*Cicer arietinum*) and black-eyed pea (*Dolichos*).

The adult is approximately half an inch long with a wing span of four-fifths of an inch, and is light brown with irregular patches of chocolate-coloured scales on the forewings, extending from the middle to the outer edge, the largest patch occurring at the anal angle. The hind wings are almost translucent, edged with grey. The underside of the wings of the female is noticeably darker than that of the male. The male and female are equal in size. The sexes can be readily distinguished by the presence, in the male, of a fringe of dark scales on the inner surface of the basal segments of the antennae, and a tuft of fine hairs on the second segment of the labial palps.

Females emerge from pupae of similar age one or two days before the males. Of 1,509 adults emerging from field-collected larvae during July and August 1953, 53 per cent. were females.

The length of life of adults in the laboratory with food in the form of sugar solution and without food (40 individuals of each type) was: —

	Days		
	Min.	Average	Max.
Males with food	1	11	20
Males without food	1	3	5
Females with food	1	12	16
Females without food	1	3	6

Ten females caged with pods and sugar solution laid 1, 3, 7, 9, 9, 27, 35, 72, 87 and 113 eggs, respectively, an average of 36·3 per female. Eggs were occasionally deposited during the first night after emergence, but usually not until the second night, and were laid indiscriminately on the pods and on the cloth mesh of the cage.

In the field, the eggs are laid singly on the young pods or on the sepals of the flowers. Generally one or two eggs are deposited on each pod, but when pods are scarce as many as 20 eggs may be laid on a single pod. The egg is ovoid, approximately 0·6 mm. long and 0·4 mm. wide, creamy white at first, gradually darkening to yellow and then to a brownish orange before hatching. The chorion is sculptured, giving the appearance of irregular minute pits over the entire surface.

The egg hatches on the third or fourth day after oviposition and the larva wanders over the exterior of the pod for several hours, feeding on the surface pubescence, before eating its way into the pod, where it feeds on the developing seeds. As it feeds, frass is deposited in the form of pellets and webbed together with silken threads. Larval development may be completed in one pod unless the pods are small or another larva is present. Under these circumstances the partly grown larva leaves the pod and enters another, closing the entrance hole with fine white webbing.

There are five larval instars. The head capsule and cervical shield are blackish in the first three instars and brownish in the fourth and fifth. The body is pallid at first, becoming green after feeding has begun and later striped with irregular longitudinal streaks of darker pigment. Towards the end of the fifth instar the dark streaks disappear and many of the larvae assume a reddish tinge, the others remaining uniformly green.

When full-grown, the larva leaves the pod and drops to the ground, where it constructs a thin cylindrical cocoon of fine webbing just below ground or, less frequently, in the surface trash. Before construction of the cocoon the larva is approximately 12 mm. in length but contracts to 10 mm. and turns pale green before pupating. The pupa is 9·4–10·0 mm. long and 3·3–3·6 mm. wide, light green, later becoming dark brown. The genital pore is on the eighth segment in the female and on the ninth in the male. The larval, prepupal and pupal stages are completed in 14–16, 2 and 7–10 days, respectively.

Occasionally diapause occurs in the pupal stage. Development may be arrested for as long as two months, but more frequently begins again after 20 days. Diapause may be correlated with the dry season, a factor also affecting the production of green pods. Hence larvae developing as the production of green pods ceases would be forced to feed on drier seeds than usual. Squire (1940) reported that diapause of *Platyedra gossypiella* (Saund.) is induced by a lowering of the moisture content of the food.

Parasites of *Ancylostomia stercorea.*

Although several thousand eggs of *A. stercorea* were collected and held for parasite emergence during the period 1952–1954, no egg-parasites were found. The following parasites were reared from larvae of *Ancylostomia*: the Braconids, *Apanteles eticllae* Vier. (subsp. *isolatus* Mues.), *Phanerotoma bennetti* Mues., *Bracon thurberiphagae* (Mues.) and *Bracon cajani* Mues., the Ichneumonid, *Eiphosoma annulatum* Cress., and the Bethylid *Perisierola* sp.; an undetermined species of Tachinid, and a Mermithid nematode, possibly *Mermis albicans.*

The life-histories of the Hymenopterous parasites are given below, the terminology used by Short (1952) being adopted. Where possible, Muesebeck, Krombein & Townes (1951) have been followed in nomenclature.

Records for the duration of the various stages of the parasites were obtained at room temperatures, which fluctuated diurnally and with the weather. The

British Caribbean Meteorological Service unit at the Imperial College of Tropical Agriculture recorded 70·9 and 87·6°F. for the mean minimum and mean maximum temperatures for 1952 and 71·2 and 86·6°F. for 1953.

Apanteles etiellae **Vier. (subsp.** *isolatus* **Mues.) (Braconidae, Microgasterinae).**

The subspecies *isolatus* is structurally similar to the typical subspecies but differs in having a hyaline stigma as contrasted with a fuscous stigma. Muesebeck lists the distribution of *isolatus* as British Guiana, Trinidad, Grenada, Dominica and Virgin Islands, most of the records having been obtained from the present investigations.

Although *Ancylostomia stercorea* is the only host record of this subspecies, Muesebeck, Krombein & Townes (1951) record *Etiella zinckenella* (cited as *E. schisticolor* (Zell.)), *Psorosina hammondi* (Ril.), *Canarsia* sp., *Ufa rubedinella* (Zell.) (cited as *Elasmopalpus rubedinellus* (Zell.)) and *Olycella junctolineela* (Hulst) as hosts of the typical form.

Life-history and habits.

On emergence the female attacks hosts readily. No preoviposition period occurs and mating is not essential, unmated females producing only male progeny. The act of copulation is similar to that of *Apanteles solitarius* (Ratz.) described by Parker (1935). The male approaches the female and if not repulsed mounts on her back and engages the genital organs for a period of five to ten seconds. However, if the female does not wish to mate, the male is brushed off as the female moves away.

Adults are very active and if starved die in less than 24 hours after emergence: when supplied with sugar solution they live for several days. The minimum, average and maximum length of life determined from 50 males and 50 females fed with sugar solution in a 4½″ × 4½″ × 3″ cloth-sided wooden cage was 2, 6 and 12 days for females and 1, 6 and 10 for males. Like *A. solitarius*, adults live longer when held in complete darkness, the minimum, average and maximum lengths of life of 50 females under these conditions being 1, 8 and 18 days.

In the field, an ovipositing female locates the host entrance hole in a pod, inserts the ovipositor, and probes about with a series of rapid thrusts until a suitable larva is found, and remains motionless for a few seconds until the egg is deposited; she then withdraws the ovipositor and cleans it and her antennae with her tarsi before searching for another host. Eggs are laid only in first- to third-stage larvae.

The larva develops as a solitary endoparasite, emerging when the host reaches the fourth stage. The immature stages are completed in 14–18 days, the egg, larval, and combined prepupal and pupal stages being 2, 6–8 and 6–8 days, respectively.

After hatching, the larva remains small until the host reaches the fourth stage. The parasite then develops rapidly and consumes the entire body-contents of the host before emerging and spinning its cocoon.

Before the host larva is killed it generally chews a hole in the pod but succumbs before escaping. After emerging from the cocoon by cutting the circular cap, the adult parasite uses this hole to reach the exterior, and when no hole has been made is apparently unable to escape. This presumption is based on the frequent discovery of dead adults in pods.

Description of stages.

Egg: when newly deposited, shortly pedunculate at posterior end, dilated at the other (fig. 1, A), length with peduncle *ca.* 0·5 mm., greatest width 0·15 mm., chorion smooth, transparent. The egg expands considerably after deposition. *First-stage larva*: on hatching approximately 0·6 mm. long and 0·2 mm. broad.

Head blunt, occupying about one-third of total length, and wider than the other segments. Body tapering gradually to a pointed caudal horn; anal vesicle not protruded in newly hatched larva but appearing towards the end of the first day, and becoming proportionately larger as the larva increases in size, whereas the

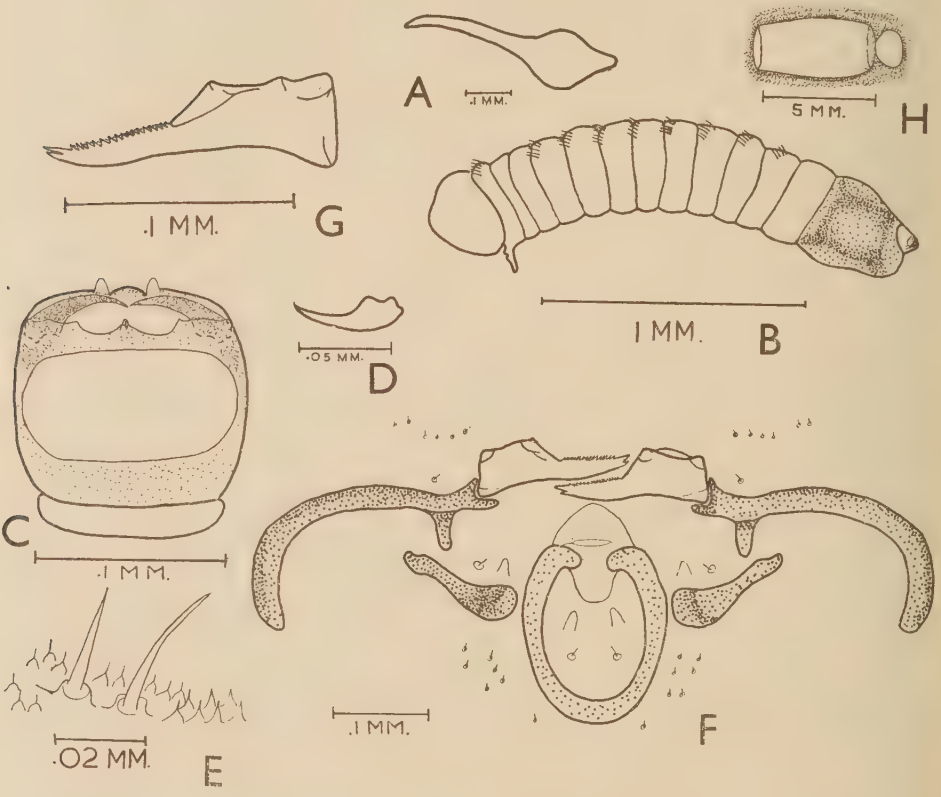


Fig. 1.—*Apanteles etiellae isolatus* Mues. A, egg; B, first-stage larva, almost fully grown (lateral view); C, head of first-stage larva (ventral view); D, mandible of first-stage larva; E, skin armature of last-stage larva; F, head sclerites of last-stage larva; G, mandible of last-stage larva; H, cocoon.

caudal horn becomes proportionately smaller. Body segmentation indistinct, only seven or at most eight abdominal segments distinguishable in newly hatched larva, but later ten. An irregular transverse row of stout colourless spines dorsally on abdominal segments 1–7 and 10 (fig. 1, B). A few smaller spines present on third thoracic segment. Head apparently not increasing in size, and towards the end of first stage considerably narrower than the following segments (fig. 1, C); labral processes well developed, concealing mandibles and mouth orifice; mandibles simple, comma-shaped and sharply pointed (fig. 1, D). First thoracic segment swollen and lobed towards the end of first stage; anal vesicle wider than body segments and caudal appendage barely evident at the end of the first stage. *Second-stage larva*: anal vesicle very large and caudal appendage

obsolete. Mid-gut plainly visible as it assumes colour of host body-fluid. Silk glands well developed, extending into abdominal segments. Tracheal trunks present but no open spiracles. Mandibles poorly defined and unpigmented, small, without teeth, and obscured by the labral processes. First exuvia usually adhering to the last abdominal segment anterior to the anal vesicle. *Third-stage larva*: on emergence from host, larva moults into third stage leaving first and second exuviae inside host near emergence hole. Before spinning cocoon, larva is about 5·5 mm. long but only 4·5 mm. after cocoon is completed. Each segment of body densely spinulose and encircled by a row of larger setae (fig. 1, E). Mandibles and sclerites of head well defined and as in *A. tirathabae* Wlkn. figured by Short (1953) (fig. 1, F); mandible bifid at the tip, with 18 teeth on the upper edge (fig. 1, G). This species runs to group S. or U. in Short's (1953) classification of *Apanteles* larvae. *Cocoon*: white, of typical round-ended cylindrical *Apanteles* type, about 5 mm. long and 1·5 mm. wide (fig. 1, H). *Pupa*: white at first, gradually darkening to black, similar to that of *A. congregatus* (Say) figured by Fulton (1940).

Laboratory rearing.

This species breeds fairly readily in the laboratory, although females are reluctant to mate. The presence of fresh frass excites the females and successful copulation frequently occurs while the female is searching the frass for host larvae. Parker (1935) described a method for breeding *A. solitarius* which is easily adapted to this species. Larvae exposed to four or five mated females in a glass vial are removed by means of a camel-hair brush when parasitised, and replaced with others. As the females attack the host larvae readily, usually requiring only a few seconds to locate and parasitise them, several hundred larvae can be exposed by one worker in the course of a day. Parasitised larvae are then placed in glass tubes with a few pigeon peas until the parasites emerge and construct cocoons. Although mortality among host larvae is high, large numbers of parasites may be reared in this way.

Phanerotoma bennetti **Mues. (Braconidae, Cheloninae).**

The adult has been described by Muesebeck (1955) who records specimens from Trinidad and British Guiana. No other natural hosts of the species, other than *Ancylostomia stercorea*, are recorded.

Life-history and habits.

Females begin to search for hosts immediately after they emerge from the cocoon and oviposit freely as soon as suitable hosts are located. The progeny of unmated females are males. Mating takes place readily. The male approaches the female and attempts to mount on her back. If the female refuses to mate she raises her wings and moves away, otherwise the male engages her genital organs and releases all other contact. Copulation is completed in 30 to 50 seconds. Males will mate with several females in quick succession and may mate with the same female more than once in the course of a day. The adults are hardy and survive for several days if provided with food in the form of sugar solution. As determined from ten males and ten females kept in a small cloth-sided wooden cage and supplied with sugar solution, the minimum, average and maximum lengths of life for the females were 3, 8 and 35 days, and for the males 2, 9 and 12 days. Females predominate in field-collected material, 61·9 per cent. of the adults sexed during 1953 being females.

The female deposits her eggs in the eggs of the host. When searching for hosts, the female runs quickly over the pod exploring the surface with her antennae. When she senses the presence of a host egg the antennae vibrate more rapidly until they touch it. After examining the egg briefly, first with the

distal segments of the antennae and then with the basal ones, the female moves forward slowly until the tip of the ovipositor, which is extended downward and forward, touches the egg. It pierces the chorion and the parasite egg is laid immediately. The period of examination and oviposition is very brief. A female was seen to deposit eight eggs in two minutes, and on another occasion, when a pod bearing 47 eggs was offered to a female, 38 of them were parasitised in less than one hour. Although more than one egg may be laid in a host, only one parasite develops; the others fail to hatch or die shortly afterwards.

Dissection of host eggs and small larvae shows that the parasite egg hatches before that of the host. The parasite larva remains small until the host has become quite large, and parasitised host larvae cannot be readily separated from non-parasitised ones until larval feeding is complete. At this time the host is similar in appearance except for size to the normal full-grown larva. However, the head capsule only measures the same as that of the fourth-stage larva, but as Bradley & Burgess (1934) pointed out in the case of larvae parasitised by *Chelonus annulipes* Wesm. the head capsules were distinctly smaller than those of non-parasitised larvae of the same instar. It is concluded therefore that the host is in the fifth instar when the parasite issues from the host.

Before it dies, the host larva leaves the pod, drops to the ground and constructs a cocoon. At this time the host appears well nourished and except for its smaller size is similar in appearance to an unparasitised larva about to pupate.

When the host larva drops to the ground the parasite is still in the first instar but moults into the second shortly afterwards. Two days later it changes to the final instar and begins to emerge from the host. It pierces a hole in the lateral wall of the third thoracic or first abdominal segment of the host and works its way out until only its last abdominal segment remains inside. The parasite

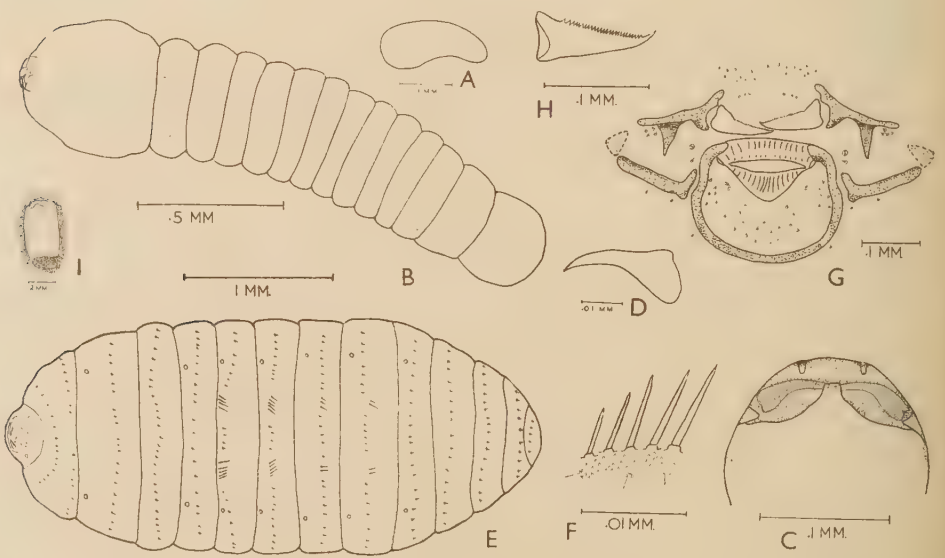


Fig. 2.—*Phanerotoma bennetti* Mues. A, egg; B, first-stage larva (ventral view); C, head of first-stage larva (ventral view); D, mandible of first-stage larva; E, last-stage larva (dorsal view); F, skin armature of last-stage larva; G, head sclerites of last-stage larva; H, mandible of last-stage larva; I, cocoon.

then makes several incisions in the abdominal segments of the host and feeds externally until only the head and integument of the host remain.

The parasite constructs a cocoon inside that of the host and pupates. If the host cocoon is removed, the larva is unable to construct a cocoon unless placed in a similar confined space; a small number will then spin normal cocoons. Larvae that fail to construct cocoons frequently pupate but seldom transform into adults.

The life-cycle of *P. bennetti* lasts 20–26 days when it develops on *Ancylostomia*. The egg, larval, and combined prepupal and pupal stages are 2, 10–16, and 8–10 days, respectively. However, the life-cycle takes 40 to 50 days when *Ephestia cautella* (Wlk.) is used as a host for laboratory breeding (see below), *Phanerotoma* synchronising its development with that of the host.

Description of stages.

Egg: white, smooth, at first approximately 0·2 mm. long and 0·1 mm. wide, elongate-ovoid in shape with both ends bluntly rounded (fig. 2, A). *First-stage larva*: during the first instar the larva increases greatly in size and changes considerably in appearance. When newly hatched, larva is 0·20–0·24 mm. long and about 0·6 mm. wide at head which is wider than the other segments. Seven body segments distinguishable in newly hatched larva but later 13. Anal vesicle evaginating shortly after eclosion and gradually enlarging. Integument with several rows of translucent spinules (fig. 2, B). Near the end of first stage, head relatively very small and first thoracic segment approximately three times as long as those succeeding it. Mouthparts ventral, labrum large, with two movable processes (fig. 2, C); labium relatively small with a rectangular projection. Mandibles approximately 0·027 mm. long, brown, comma-shaped and simple (fig. 2, D). *Second-stage larva*: few distinct features are present in this stage. Body round, elongate and free of spines, anal vesicle well developed; mouthparts appearing as raised areas and not noticeably sclerotised, mandibles obscure. Contents of mid-intestine almost colourless (*cf.* green in second stage of *Apanteles etiellae isolatus*). First cast skin, bearing the mandibles, frequently adherent to last abdominal segment of second-stage larva. *Third-stage larva*: when fully fed approximately 7·5 mm. long and 2 mm. wide, cylindrical, increasing in width posteriorly to the sixth abdominal segment and then tapering caudad. Integument densely spinulose with an irregular row of larger spines on each body segment except last, and a few long brown chitinised spines, variable in number and arrangement, dorsally on the second to the fifth abdominal segments (fig. 2, E, F). Spiracles present on second thoracic and first six abdominal segments: mouthparts well defined and like those of *Ascogaster quadridentata* Wesm. (Rosenberg, 1934) and *Chelonus* sp. (Short, 1952). Labial ring, stipital sclerite and broad short hypostoma heavily sclerotised (fig. 2, G); hypostomal spur flat and very broad at base. Setae present on labium and above labrum, behind each hypostomal spur (4), and near the maxillary palps (1). Labrum with six sensoria marginally, labial and maxillary palps apparently terminating in two blunt circular sensoria. Mandibles each about 0·1 mm. long, broad at base, distally acuminate, with long fine teeth on upper edge (fig. 2, H). *Cocoon*: normally enclosed in webbing constructed by the host, cylindrical, 7·5 mm. long and 3 mm. wide (fig. 2, I), chartaceous, constructed of glistening white strands closely woven to give a smooth inner surface, and encircled with a white band of loosely woven strands. *Pupa*: white, later assuming brownish coloration of adult. As with *Chelonus annulipes* (Vance, 1932) the end of the abdomen is immersed in the viscous brown meconium excreted by the mature larva.

Laboratory rearing.

Owing to the heavy mortality of small host larvae it is difficult to breed this species on *Ancylostomia*. Attempts were therefore made to find a host suitable

for laboratory propagation. Adults of *Corcyra cephalonica* (Stnt.), *Plodia interpunctella* (Hb.) and *E. cautella*, collected at a nearby feed mill, were allowed to oviposit over flour. The eggs were sifted from the flour and placed on cardboard moistened with water where they adhered firmly when the water evaporated. The eggs were then exposed to females of *Phanerotoma* in 4″ × 1″ glass tubes. Eggs of *Plodia* and *Ephestia* were readily attacked, but those of *Corcyra* were ignored even when placed in tubes with females that had previously been ovipositing in *Ephestia* eggs. Cards bearing the exposed eggs were placed in containers partly filled with flour and left undisturbed. The *Plodia* larvae died shortly after hatching, possibly because the food was unsuitable. *Phanerotoma* adults emerged from the *Ephestia* culture 40 to 50 days later. Only small numbers were bred in the laboratory on *Ephestia* but the results indicated that the method described by Bradley (1941) for rearing *Chelonus annulipes* in the laboratory on *Anagasta kühniella* (Zell.) could be used satisfactorily.

The methods described for rearing *Eiphosoma annulatum* from field-collected larvae of *Ancylostomia* (see below) were used to obtain sufficient numbers of this species for shipment to Mauritius.

Eiphosoma annulatum **Cresson (Ichneumonidae, Ophioninae).**

Muesebeck, Krombein & Townes (1951) listed *Eiphosoma bruesi* Cushm. as the sole synonym, and *Mimorista flavidissimalis* (Grote) as the only host. Fennah (1947) records *E. annulatum* from *Zinckenia fascialis* (Cram.). Muesebeck, Krombein & Townes list the distribution of this species as south Texas, West Indies, Mexico and south to Argentina.

The female has been described by Cushman (1920) as that of *E. texanum* Cress. (mis-det.) and *E. bruesi*, but the male is apparently undescribed. The coloration of the head, thorax and legs is similar in both sexes. The abdomen of the male is marked with alternate bands of black and brown whereas that of the female is dominantly brown with variable, less conspicuous, black markings.

Life-history and habits.

The adults are active and feed readily on sugar or honey solution in the laboratory. As determined from 40 females and 40 males, the minimum, average and maximum number of days that the females lived were 2, 10 and 28 days, and the males 1, 7 and 18 days.

Copulation has not been observed and although mating is not essential there is a preoviposition period of five or six days. Unfertilised eggs produce only male progeny.

The act of oviposition is rapid, requiring less than ten seconds once the host is encountered. The female explores the surface of the pod until a larval tunnel is found. She inserts her ovipositor and probes about until the larva is located. The tip of the ovipositor is thrust into the larva and an egg deposited in the body cavity. The egg may be laid in any of the body segments but is generally found in the posterior ones probably because these are encountered most frequently by the female. The female does not drill through the pod but attacks the host through the larval tunnel.

The female oviposits in first- to fourth-stage larvae. Usually one egg is laid in each host, but as many as three eggs have been observed in one first-stage larva. Only one parasite can complete its development in a single host. The fate of the additional eggs is not always the same. The following observations were made during the dissection of field-collected larvae: one first-stage host contained three eggs; one second-stage host contained one first-stage larva and one collapsed egg in the abdominal region and one egg containing a live larva in the thoracic region; one third-stage host contained one collapsed egg and two larvae, the larger of which appeared injured but the small one was active; one last-

stage host contained one large first-stage larva of *Eiphosoma* and one small dead one. The dead individuals were frequently marked as though injured by the surviving ones and had not died as a result of physiological changes in the host caused by the presence of other larvae.

After hatching, the larva begins to feed before it leaves the egg, the caudal appendage remaining bent forward (fig. 3, B). It remains small until the host reaches the last larval stage, and then develops rapidly, changing into the second stage about the time the host ceases to feed. If the host is attacked in the first or second stage it develops to the fifth stage but is stunted. If attacked in the third or fourth stage it attains full size before the parasite emerges.

The parasitised larva leaves the pod and constructs a cocoon similar to that of an unparasitised one. When the larva emerges from the host it spins a cocoon inside that of the host.

The life-cycle is completed in 26–33 days. The egg hatches on the fourth day, the cocoon is constructed 11–16 days later, and 11–15 days are spent in the cocoon. The adult escapes by chewing an irregular hole in the end of the cocoon. The males begin to emerge a day before the females. Males predominate slightly in collections reared from the field-parasitised larvae: 56 per cent. of the adults reared during 1953 were males.

Description of stages.

Egg: elongate, ovoid, with unsculptured chorion, about 0·4 mm. long and 0·12 mm. broad (fig. 3, A), dull white becoming brown about 24 hours after deposition. *First-stage larva*: (fig. 3, B) caudate and folded within egg so that tip of caudal appendage is near mandibles. Each body segment at first encircled with two transverse folds which later disappear. (Bradley & Burgess (1934) refer

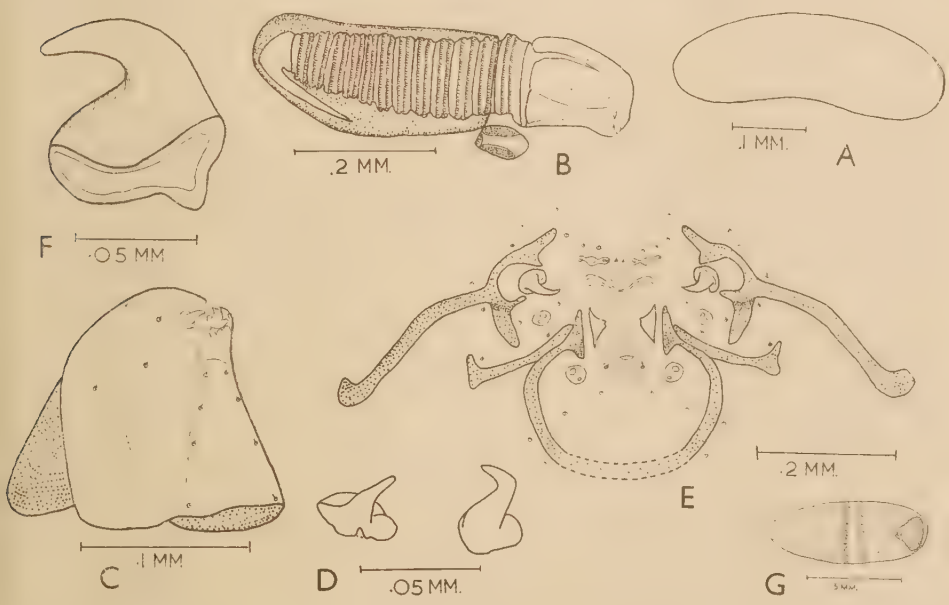


Fig. 3.—*Eiphosoma annulatum* Cress. A, egg; B, first-stage larva emerging from egg; C, head capsule of first-stage larva (latero-ventral view); D, mandibles of first-stage larva; E, head sclerites of last-stage larva; F, mandible of last-stage larva; G, cocoon.

to similar folds, termed " scallops ", on the first-stage larva of *Cremastus flavoorbitalis* (Cam.) which permit the body to enlarge more readily.) Caudal appendage almost half length of remainder of body but proportionately shortening as the larva develops. Head capsule heavily sclerotised, brown and flattened ventrally; dorsal surface with two grooves extending forward from the posterior edge for a considerable distance (fig. 3, C) and widening posteriorly as the larva develops; dorsal and lateral portions of head capsule widely separated near end of first stage. Two rows of three setae on ventral surface of head and a few setae on lateral portions. (Bradley & Burgess (1934) and Rosenberg (1934) describe similar setae on other Ophionines.) Mandibles heavily sclerotised, comma-shaped and without teeth (fig. 3, D). Length with caudal appendage about 0·7 mm. on hatching, increasing to 2·7 mm. prior to first moult. *Second-stage larva*: indistinctly segmented, devoid of caudal appendage; spiracles absent, integument unornamented. Unlike the first- and third-stage larvae no distinct sclerotisation visible in head; mandibles obscure. *Third-stage larva*: about 8·0 mm. long and 2·5 mm. wide on emergence from host, integument bluntly tuberculate, devoid of prominent spines or setae except on head. Nine pairs of spiracles present, the first posterolaterally on prothoracic segment and the others anterolaterally on first eight abdominal segments. Head with pleurostoma, hypostoma and sclerotic spur and stipital sclerite distinct (fig. 3, E); labial sclerite heavily sclerotised laterally but less so ventrally. Labial and maxillary palps each terminating in three circular projections which vary in shape and size with individual larva. Labrum with two sensoria, each having four papillae also variable in shape and size. Setae as shown in fig. 3, E. Mandibles approximately ·07 mm. long, stout, comma-shaped and simple (fig. 3, F). *Cocoon*: thin and subchartaceous, constructed of tightly spun glistening strands, 7 to 9 mm. long and approximately 3 mm. wide, brown with a central white band which is frequently bordered by indefinite bands of dark brown (fig. 3, G). *Pupa*: white at first but darkening a few days before emergence to coloration of adult.

Laboratory rearing.

Attempts to breed *Eiphosoma annulatum* in the laboratory were not successful as adults could not be induced to mate. No copulation took place when males and females of varying ages were placed in glass tubes or in cloth-sided cages of dimensions $4\frac{1}{2}'' \times 4\frac{1}{2}'' \times 3''$, or $9'' \times 12'' \times 14''$. In the field, both sexes were frequently observed around flowering plants, and it is possible that mating takes place at this time.

Host larvae placed between layers of cheese-cloth and exposed to unmated females in small cages were readily parasitised, the resulting progeny being males.

The following method was developed to facilitate the collection of cocoons of *Eiphosoma* and *Phanerotoma* from field-collected host larvae. Infested pods were placed in jars containing sand or in wire-bottomed trays over boxes containing a layer of sand $\frac{3}{4}''$ thick. Larvae parasitised by *Eiphosoma* and *Phanerotoma* as well as unparasitised larvae formed cocoons in the sand. Four or five days later the sand was sifted through a screen leaving the sand-encrusted cells containing the parasite cocoons and host pupae.

Experiments were carried out to determine whether or not the methods described by Martin & Finney (1946) for the removal of the host cocoons and the separation of parasite cocoons from the host pupae were applicable. These authors dissolved the silk cocoons of *Gnorimoschema operculella* (Zell.) by immersion in a dilute solution of sodium hypochlorite and separated the host pupae from the cocoons of *Macrocentrus ancylivorus* Rohw. by immersion in a solution of 95 per cent. ethyl alcohol. In the present investigations the household bleach disinfectant, ' Klene ', was found satisfactory when used without

dilution. The host cocoons dissolved in ten minutes, freeing the host pupae and parasite cocoons. These were washed in water, and when placed in 95 per cent. ethyl alcohol the host pupae settled to the bottom and the parasite cocoons floated to the surface. After removal from the alcohol, both parasite cocoons and host pupae were washed in water. No increase in mortality due to these treatments was noted.

Bracon thurberiphagae (**Muesebeck**) (**Braconidae, Braconinae**).

The sole synonym listed by Muesebeck, Krombein & Townes (1951) is *Microbracon thurberiphagae* Mues. The types of the species were reared from *Thurberiphaga diffusa* (Barnes). Fennah (1947) records *B. thurberiphagae* from *Maruca testulalis* and *Ufa rubedinella* (cited as *Elasmopalpus rubedinellus*) in the Lesser Antilles and Trinidad. During the present investigation it has been reared, as well as from *Ancylostomia*, from *Hellula phidilealis* Wlk. on cabbage and an unidentified Gelechiid on tomato. It has been reared from collections of *Ancylostomia* from British Guiana, Grenada, Dominica, Montserrat and Antigua. Muesebeck, Krombein & Townes list the distribution in the United States as Arizona and Texas.

The number of segments in the antennae of the type series was 21–23 (Muesebeck, 1925) whereas in material reared from *Ancylostomia* the number varied from 20 to 30. This species is readily separated from *Bracon cajani* (see below) by the slightly smaller size, darker over-all colour and more extensive markings of black. In the female the ovipositor is also much shorter.

Life-history and habits.

B. thurberiphagae is a gregarious ectoparasite attacking third- to fifth- and occasionally second-stage larvae of *Ancylostomia*. A preoviposition period of four to five days occurs before egg-laying, during which the females paralyse hosts and feed on the body juices. Mating takes place readily when newly emerged females are placed with males that are two to three days old. The progeny of unmated females is male.

In the laboratory, adults live from one to 28 days if supplied with sugar solution, but die in less than four days without food.

Males predominate slightly, at 55·4 per cent., in specimens reared from field collections during July and August 1953. In masses of cocoons containing both sexes, females outnumber males (about 2:1) but broods containing only females are seldom encountered, whereas those producing only males are common; hence the over-all predominance of males. It was not ascertained whether mated females produce only male progeny in certain broods or whether all of the cocoon masses producing only males are the progeny of virgin females.

When searching for a host, the female alights on a pod and spends several hours examining it. She frequently pauses for several minutes with the antennae touching the pod but makes no effort to insert the ovipositor. A similar observation was made by Nelson & Farstad (1953) on *Bracon cephi* (Gah.). The female stings the host through the larval entrance hole or drills through the pod, a procedure lasting for several minutes. Several holes may be drilled before the larva is finally stung. If the attack is made through the host entrance the female may partially enter the pod and feed on the body-fluids of the host. No feeding tubes similar to those described by Genieys (1925) were noted.

One to 12 eggs are laid, usually near but sometimes on the host. The time spent in locating the host and depositing the eggs is often five to six hours. Occasionally two females will deposit eggs near the same host.

The eggs hatch 24 to 28 hours after deposition and the larvae are capable of moving several millimetres to reach the host. They crawl over the host, feeding externally, each larva making several punctures before feeding is complete.

Three to four days after hatching, they complete feeding, construct their cocoons within the pod and pupate. Nine to ten days after pupation the adults emerge, those from each brood usually within the space of 24 hours. They escape by chewing holes in the cocoons and through the pods if necessary.

Description of stages.

Egg: whitish, semi-transparent, unsculptured, glistening, elongate, slender and slightly curved with tapering rounded ends, one more pointed than the other (fig. 4, A), 0·72 mm. long and 0·18 mm. wide. *First-stage larva*: on hatching

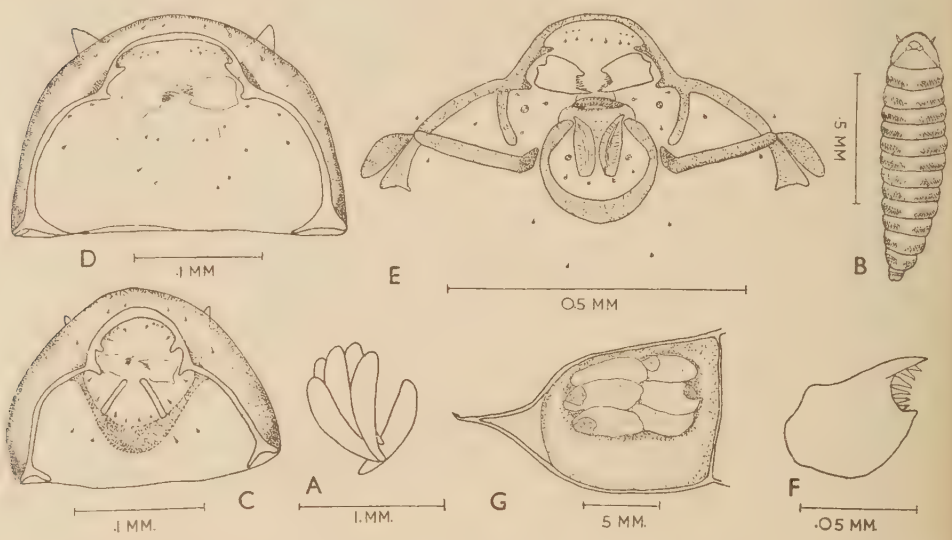


Fig. 4.—*Bracon thurberiphagae* (Mues.). A, eggs; B, first-stage larva (ventral view); C, head capsule of first-stage larva (ventral view); D, head capsule of third-stage larva (ventral view); E, head sclerites of last-stage larva; F, mandible of last-stage larva; G, cocoon mass in pod.

approximately 0·72 mm. long and 0·2 mm. wide; first twelve body segments each with a transverse band of short, slightly curved spines, narrowly incomplete dorsally and ventrally (fig. 4, B), and also with a few larger spines. Spiracles present on first and fourth to eleventh body segments; average width of atrium 0·006 mm. Head capsule lightly sclerotised and with a few scattered setae (fig. 4, C); mandibles sharply pointed and with four small teeth; antennae blunt and moderately long. *Intermediate-stage larvae*: in each succeeding stage head capsule becoming less distinct (fig. 4, D); mandibles of second stage with four teeth and those of the third and fourth five teeth; approximate lengths of mandibles of second-, third- and fourth-stage larvae 0·040 mm., 0·050 mm. and 0·058 mm., respectively. Nine pairs of spiracles present on same segments as those of first-stage larva; approximate diameter of spiracular openings of the various stages are:—second, 0·012 mm., third, 0·017 mm. and fourth, 0·021 mm. *Fifth-stage larva*: similar to that of other species of *Bracon* described by Glover (1934) and Parker (1951). Integument densely spinulose and each segment bearing several setae. Spiracles on the first thoracic and first eight abdominal segments; average diameter of spiracular opening 0·023 mm. Head sclerites complete in number, well defined, brown (fig. 4, E), similar to those of *Bracon terebella* Wesm. figured by Short (1952); labrum with two pairs of sensorial

papillae and three pairs of setae, labial palps terminating in two circular sensoria; two pairs of setae near labial palps and two pairs ventrad to labial sclerite; maxillary palps each slightly sclerotised distally and with two unpigmented circular sensoria; two setae on each maxilla; mandibles robust, with six teeth, 0·064 mm. from tip of blade to base (fig. 4, F). *Cocoon*: spun against side of pod, light brown, generally those of each brood loosely matted together (fig. 4, G). Texture, thickness and colour of the cocoon variable, sometimes very thin and papery, sometimes much heavier and also darker. *Pupa*: whitish when first formed, changing later to yellow, thorax and head gradually darkening to brown.

Laboratory rearing.

All attempts at mass breeding of this species in the laboratory were unsuccessful although several types of breeding cages and techniques were tried. Mated females were readily obtained but failed to oviposit satisfactorily. Although a few progeny were obtained these were less than the original number of adults.

A satisfactory method of handling field-parasitised material was developed. Infested pigeon peas were opened and any host larvae with *Bracon* eggs or larvae were removed and placed in $1\frac{1}{2}'' \times \frac{3}{8}''$ glass vials, two or three parasitised larvae per vial. Plugs of cotton-wool were inserted to close the vials until the parasite larvae had formed their cocoons; they were then removed. Mortality was extremely low, even among small parasite larvae and eggs, when handled carefully. Several thousand parasites were reared in this manner.

Bracon cajani **Mues. (Braconidae, Braconinae).**

The adult has been described by Muesebeck (1955). *Bracon cajani* has been reared only from Trinidad in the present investigation.

Life-history and habits.

The biology and habits of *Bracon cajani* are without notable exceptions similar to those of *Bracon thurberiphagae* described above.

Description of stages.

Egg: slightly more elongate and thinner than that of *B. thurberiphagae*, approximately 0·8 mm. long and 0·16 mm. wide, smooth and glistening (fig. 5, A). *First-stage larva*: when newly hatched approximately 0·76 mm. long and 0·16 mm. wide. First twelve segments each completely encircled medially with rows of short slightly curved spines (fig. 5, B), which are more prominent on thoracic and first abdominal segments becoming less distinct and fewer on last abdominal segment; twelfth body segment with only eight or ten spines and thirteenth unarmed; spines more numerous and prominent than in *B. thurberiphagae*. Mandibles and spiracular openings of same size as those of *B. thurberiphagae*. *Intermediate-stage larvae*: three intermediate stages, not readily distinguishable from corresponding stages of foregoing species. *Fifth-stage larva*: very similar to that of *B. thurberiphagae*, including position of head sclerites, arrangement of setae on head and number of teeth on mandibles. Silk press similar in shape but less heavily sclerotised in *Bracon cajani*. Spines of the skin armature of *B. thurberiphagae* more numerous and darker than those of *Bracon cajani*. *Cocoon*: similar to that of *B. thurberiphagae*. *Pupa*: towards end of pupal stage, females distinguishable from those of foregoing species by greater length of ovipositor.

Laboratory rearing.

This species presented the same difficulties in laboratory breeding as the previous one and adequate numbers for shipment were obtained in the same manner.

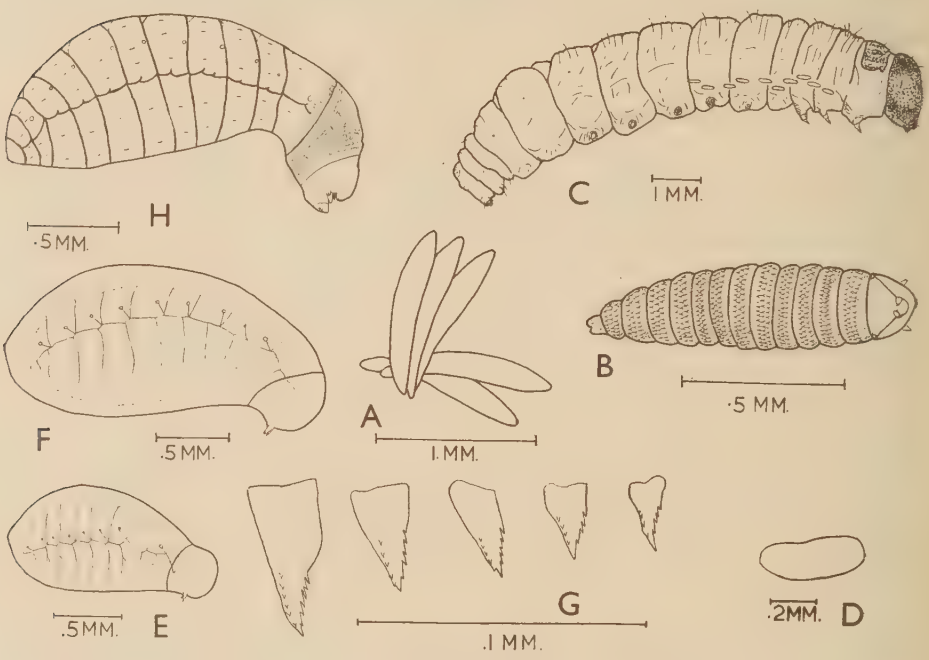


Fig. 5.—*Bracon cajani* Mues. A, eggs; B, first-stage larva (ventral view). *Perisierola* sp. C, eggs on host; D, egg; E, second-stage larva (lateral view); F, fourth-stage larva (lateral view); G, mandibles, first to fifth stages; H, fifth-stage larva (lateral view).

Perisierola **sp. (Bethylidae).**

This species was reared from collections of *Ancylostomia* larvae from British Guiana, Trinidad and Dominica. The adult may be readily distinguished from those of other parasites of *Ancylostomia* by the elongate, flattened head, the rather ant-like appearance and the black colour. It seldom flies long distances but alternately runs and flies a few inches at a time.

Life-history and habits.

Perisierola sp. is a gregarious ectoparasite. Males from a mass of cocoons emerge a few hours earlier than the females and occasionally tear open the female cocoons and enter them; more frequently the males wait until the females emerge before copulating. Copulation is a simple affair lasting only a few seconds and is not preceded by any characteristic preliminary courtship. Females may mate between successive periods of egg-laying although a single mating is sufficient to ensure the production of a high percentage of female progeny

throughout life. Females predominate in emergents from field-collected material, the ratio being 6:1.

Females live from two to five weeks if provided with hosts but survive for less than two weeks with only sugar solution for food. Although males feed readily on sugar solution they seldom live longer than seven days.

Females enter infested pigeon pea pods through the entrance made by a partly grown host larva. Inside the pod the parasite paralyses the larva by stinging it and then deposits eggs on it.

The act of subduing the host larva has been observed several times. The parasite taps the larva with her antennae and this causes it to move away. The parasite follows, and when the larva can retreat no further, crawls over the dorsum, grasps the larva with her mandibles, bends her abdomen beneath the thorax and stings the larva between the first thoracic legs. These actions are carried out despite the violent writhing of the host. The larva soon becomes quiet and the parasite examines it, biting and stinging it in several places until no movement is shown. Two or three days may pass before eggs are laid. During this period the adult feeds on the body-fluids of the host, and arranges the larva in a suitable position for oviposition. Females of *Perisierola* of varying ages that have not previously fed on host fluids do not lay eggs until three days after a host is attacked, a fact which suggests that this feeding is necessary for oviposition.

The maximum number of eggs laid by one female under observation was 67 over a period of 38 days. Eggs are placed longitudinally in an irregular row on the side of the host with the anterior end forward (fig. 5, C) and adhere firmly to the host. The number laid on one host varies from one to 14, usually being eight to ten on a large host. All larvae from the second to the full-grown stage are subject to attack but the third, fourth and fifth stages are usually chosen.

The female remains with her progeny until they are well developed, in some cases until they pupate, but if other hosts are present in the same pod they are frequently attacked.

On hatching, larvae make their feeding punctures before the egg-shell ruptures dorsally. Larval feeding takes place through the same puncture in all instars. The egg-shell and successive exuviae rupture dorsally and remain adhering to the ventral surface of the parasite larva. As the larva feeds, the head and succeeding segments gradually become embedded in the host. In the final instar the head and the thoracic segments are completely enveloped. When development is completed the larvae spin their cocoons near the host, those from each host being loosely matted together. The meconium, when passed, soaks through the end of the cocoon, fastening it more firmly to the substratum.

The life-cycle of *Perisierola* varies from 12 to 15 days. The egg stage lasts one to two days, larval feeding is completed in three to four days, the cocoon is formed the following day and adults emerge seven to nine days later.

An interesting observation on the habits of the female of *Perisierola* was recorded on 22nd February 1952. A field-collected pod was opened and found to contain three large *Ancylostomia* larvae and a female of *Perisierola*. One of the larvae had been parasitised by *Bracon* sp., five large *Bracon* larvae being present. When the pod was opened, three of the *Bracon* larvae were dislodged from the host and remained in one half of the pod. Two of these larvae had an unnatural dusky appearance and the other one appeared normal. All were alive and had reached the final larval stages but died without pupating.

The other half of the pod, containing the two live *Ancylostomia* larvae, the parasitised larva with the two *Bracon* larvae and the *Perisierola* adult, was placed in a glass vial and a cotton plug inserted to close the vial. At this time the adult was examining the parasitised larva and continued to do so for almost

half an hour. Eventually it walked into the next section of the pod, which contained a living larva partly hidden by the seed on which it was feeding. The parasite tapped the larva a few times with its antennae, which caused the larva to move. The parasite, standing on the seed, appeared to be making efforts to sting the larva, causing it to move again. The head of the larva came into view and the parasite grasped the larva laterally between the first and second thoracic segments. The larva started to squirm backwards, the end of the abdomen appearing on the other side of the seed. The parasite maintained its grip on the larva and by bracing its feet on the seed prevented the larva from escaping despite its much bigger size. The abdominal end of the larva threshed about freely, came in contact with the parasitised larva in the next section of the pod and dislodged one of the *Bracon* larvae which adhered to it. During the struggle the parasite stung its victim and released its grip. The larva stopped struggling and was unable to move when the adult examined it a few moments later.

After examining the larva for ten minutes, the parasite encountered the recently dislodged *Bracon* larva which was attempting to feed on the newly parasitised host. The *Perisierola* adult grasped it and after a struggle which moved the posterior half of the *Ancylostomia* larva, pulled it free and dragged it into the next section of the pod. The adult returned to the host and a few minutes later moved to the larva parasitised by *Bracon* and grasped the remaining *Bracon* larva with its mandibles. The larva was eventually dislodged and dragged to the section of the pod containing the other *Bracon* larva.

Returning to its own victim the adult began to remove frass from under the head of the larva, pausing occasionally to rest or to examine the larva. One hour later the parasitised larva had been straightened out, but remained partly concealed by the seed.

When examined the following morning the *Perisierola* female had laid ten eggs on the exposed right side of the host. The vial was examined at intervals during the next week. The two *Bracon* larvae attempted to construct cocoons but died before they were completed. The *Perisierola* adult died on the fourth day, having made no attempt to attack the remaining live *Ancylostomia* larva, which pupated in the cotton plug of the tube. The larvae hatching from the *Perisierola* eggs developed to the final stage but died without constructing cocoons, possibly because moisture had condensed inside the tube and the pod started to decompose.

One other instance where a *Perisierola* female had attacked a *Bracon* larva was noted. In a pod beside an *Ancylostomia* larva was a last-stage *Bracon* larva bearing a *Perisierola* egg, the *Bracon* having been paralysed. The *Perisierola* egg hatched but the larva died while still very small. As several thousand pods were opened during the investigation without finding any other evidence of interference between these species, *Perisierola* is considered as beneficial.

Description of stages.

Egg: smooth, devoid of surface ornamentation, approximately 0·55 mm. long and 0·18 mm. broad (fig. 5, D), elongate-ovoid and slightly curved. *First-stage larva*: approximately 0·55 mm. long and 0·18 mm. wide at commencement of feeding, head almost as wide as body; segmentation not evident. The protruding mandibles each 0·02 mm. long and bearing two rows of teeth. Spiracles present on second thoracic and first seven abdominal segments. At the end of the first and in succeeding instars larva pyriform, closely resembling that of *Perisierola gallicola* (Kieff.) (Silvestri, 1923). *Intermediate-stage larvae*: the second, third and fourth instars are similar in appearance (fig. 5, E, F). Segmentation indistinct and anterior segments, which are embedded in host, narrower than remainder of body; no setae are present. In second instar, eight pairs of spiracles, arranged as in first; nine pairs present in third and fourth instars, the

additional pair situated on third thoracic segment. In second stage, mandibles have two rows of four teeth, and in third and fourth two rows of five teeth (fig. 5, G). *Fifth-stage larva*: final instar approximately 3·5 mm. long and 1·2 mm. wide (at eighth body segment). Thoracic segments, elongate until feeding is completed, thickening and shortening before cocoon is spun. Lateral evaginations present on thoracic and abdominal segments towards end of instar. Several rows of spines present on first thoracic segment and anterior to spiracles on second (fig. 5, H), and a few fine setae on all thoracic and abdominal segments; several large urate cells visible through integument. Spiracles located on the second and third thoracic and first eight abdominal segments. (The variation in the number of spiracles in different instars also occurs in *Perisierola gallicola* (Silvestri, 1923).) Sclerites of the head mostly very weakly sclerotised. Labium projecting; labial palps and six prominent setae in addition to opening of silk duct present on prelabium, each labial palp with two small sensoria and one large. Each maxilla with three setae and a maxillary palp terminating in three sensoria; stipital sclerite well developed; labrum with four papillae and two small setae and on anterior edge numerous minute projections, hypostoma evident without sclerotic spur, pleurostoma and epistoma obscure. *Cocoon*: loosely woven, light brown, oblong, 4·4 to 5·2 mm. long. *Pupae*: white when newly formed, gradually darkening to black before emergence of adult.

Laboratory rearing.

Best results were obtained by placing a mated female in a three-inch diameter glass-topped cardboard pillbox containing a layer of soil, a few green pigeon peas and three large host larvae. Usually all of the larvae were paralysed in three days and eggs had been deposited on one or more. Larvae were removed and replaced by others every three days or so. The following record of one female indicates the frequency of egg-laying.

Date	No. of hosts exposed	No. of hosts killed	No. of hosts with eggs	Total eggs
10.ii.54	3	3	1	13
14.ii.54	3	2	1	4
16.ii.54	3	2	1	6
19.ii.54	3	2	1	8
23.ii.54	3	3	1	8
25.ii.54	3	1	1	5
1.iii.54	3	1	1	4
3.iii.54	Female dead			

When the above method for rearing *Perisierola* was employed, each parasitised host larva was carefully removed and placed in a small glass cell consisting of ½″ length of ½″ glass tubing, with top and bottom made from microscope slides. Desiccation was prevented by a damp piece of blotting paper placed below the cover. For examination under a binocular microscope the cover and cell were lifted from the bottom slide which was then placed on the microscope stage without disturbing the feeding parasite larvae. The larvae constructed their cocoons without difficulty in cells of this type.

No mass breeding of *Perisierola* was carried out, but this method should prove suitable if large numbers were required.

The method described for rearing field-collected *Bracon* larvae was found satisfactory for *Perisierola* sp.

Hyperparasites.

The following hyperparasites were reared from field-collected parasite cocoons.

Family	Species	Host
Eulophidae	*Horismenus floridanus* (Ashm.)	*Bracon* spp.
	Horismenus sp.	*Apanteles etiellae isolatus*
		Bracon spp.
	Tetrastichus sp.	*Apanteles etiellae isolatus*
Eupelmidae	*Eupelmus* sp.	*Apanteles etiellae isolatus*
		Bracon spp.
Perilampidae	*Perilampus* sp.	*Apanteles etiellae isolatus*
Eurytomidae	*Eurytoma* sp.	*Apanteles etiellae isolatus*

The incidence of hyperparasites was extremely low throughout the investigation. *Horismenus floridanus*, *Horismenus* sp. and *Eupelmus* sp. were reared from most collections, but only a few specimens of *Perilampus* and *Eurytoma* were obtained during the entire period. Parasitism of *Bracon* spp. was highest in July 1953 when 2·3 per cent. of the field-collected cocoons were parasitised. Maximum parasitism of *Apanteles* occurred during the same month when 8·3 per cent. of the cocoons were attacked. The over-all parasitism of *Bracon* and *Apanteles* was less than one per cent. Although many cocoons of *Perisierola* were collected, no hyperparasites emerged. Owing to the difficulty of obtaining sufficient numbers of field-collected cocoons of *Phancrotoma* and *Eiphosoma* it was not determined whether hyperparasites of these species occurred.

Shipment of Parasites to Mauritius.

As *Etiella zinckenella* and *Maruca testulalis* are serious pests of pigeon pea in Mauritius with feeding habits similar to those of *Ancylostomia*, and as *Apanteles etiellae* and *Bracon thurberiphagae* have been recorded from *Etiella* and *Maruca*, respectively, consignments of the six primary parasites discussed above were sent to Mauritius for laboratory and field trials.

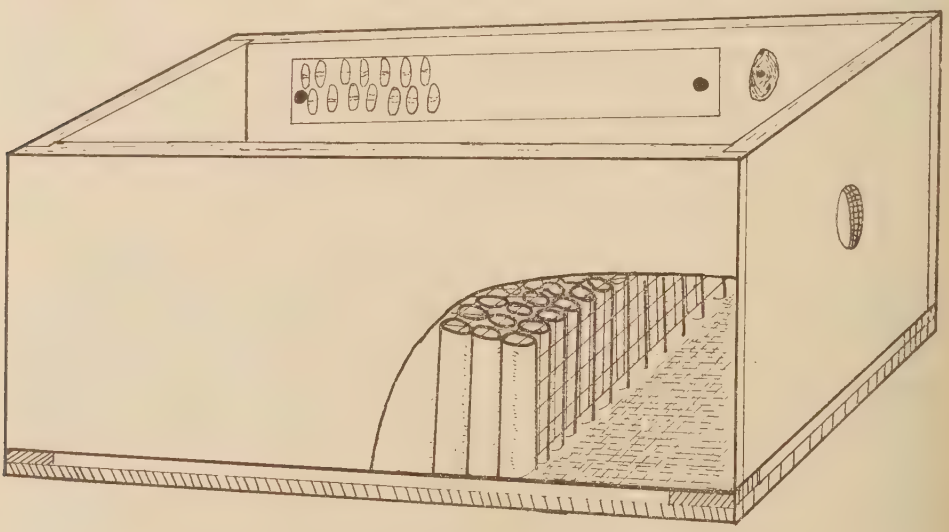


Fig. 6.—Box for shipment of parasites to Mauritius.

For shipment, a container based on that developed at the Fontana Laboratory of the Commonwealth Institute of Biological Control for shipment of Coccinellids to Bermuda and elsewhere was devised. This consists of a wooden box 8″ × 4″ × 4″, the sides and ends of ½″ white pine. The bottom of the box is covered with organdie cloth glued and tacked to the wooden sides. Outside this is placed a supporting covering of fine-mesh plastic screening. Finally, a bottom of plywood or ' Masonite ' is added, supported ¼″ away from the cloth bottom by pieces of wood at the corners, through which it is securely nailed to the sides of the box (see fig. 6). This ensures a certain amount of ventilation within the box and protects the cloth bottom. One end of the box has a hole (¾″ diameter) drilled and fitted with a cork. Into this hole a vial may be placed for collection of emergent adults. All inside joints are sealed with melted paraffin wax. A cloth-covered cotton-wool pad soaked in dilute sugar solution and a few raisins are fixed on the inside of the box to provide food for any insects that emerge in transit. To maintain a high humidity, a cloth bag containing damp sterile moss is fastened to the inside of the lid and is covered with a piece of cloth large enough to overlap the lid and be fastened by means of staples all round the upper surface.

Cocoons of the external parasites were obtained by placing field-collected *Ancylostomia* larvae bearing either parasite eggs or larvae in 1½″ × ⅜″ glass vials, two or three host larvae per vial, with cotton-wool plugs pushed well down into the vials to minimise desiccation. When the parasite larvae had spun their cocoons the cotton plugs were removed, the number of cocoons counted, and the open vials packed upright in the bottom of the shipment box, cotton-wool being placed between the vials and the wood to minimise shock. Vials were held in place by means of a piece of ¼″ square mesh gauze cut and bent to fit tightly over the open ends of the vials and to the side of the last row. This mesh was held in place by strands of wire passing through holes in the sides of the box.

Cocoons of endoparasites were obtained by placing field-collected *Ancylostomia* larvae individually in 4½″ × 1″ glass vials with green seeds of pigeon peas for food. Emergent parasite larvae spun their cocoons *in situ* and these were then carefully removed from the glass and glued onto paper strips. These strips were then pinned or glued to the inside of the shipment box. In this way both ectoparasites and endoparasites could be sent in the same shipment.

The top of the box was then nailed in place and the outside liberally painted with melted paraffin wax to seal all cracks.

Boxes prepared in this way were despatched immediately by air-express to Mauritius. Transit times varied between 6 and 17 days, averaging about 9. With the exception of the first trial shipment, living material was obtained in Mauritius from all consignments. Even with the 17-day transit time, 25 per cent. of the parasites were living on arrival, and it appeared that a most important factor is the maintenance of a relatively high humidity.

Between March and November 1953 there were sent:—of *Bracon* spp. (*B. thurberiphagae* and *B. cajani*) 35,411 examples; of *Perisierola* sp. 1,655; of *Phanerotoma bennetti* 1,892; of *Apanteles etiellae isolatus* 3,048 and of *Eiphosoma annulatum* 2,122.

Moutia (1957) has reported the successful establishment of two species, *Bracon cajani* and *Eiphosoma annulatum*. The former has been recorded annually from several localities and the latter during 1957 from one area.

Summary.

In Trinidad, the only serious pod borer attacking pigeon peas is *Ancylostomia stercorea* (Zell.). This species breeds throughout the year. The eggs are laid on the young pods and the larvae feed on the developing seeds and later pupate in the soil. The complete life-cycle requires 26–32 days.

Eight species of parasites were reared from the larvae of *Ancylostomia*. Life-history studies and rearing techniques for the six commonest species are presented.

Apanteles etiellae isolatus Mues. is a solitary endoparasite attacking first- to third-stage host larvae. It emerges from the fourth-stage host and constructs a white cocoon in the pod. The life-cycle takes 14–18 days.

Phanerotoma bennetti Mues. is a solitary egg-larval parasite. The egg is laid in that of the host, but the parasite does not complete development until the host has reached the final larval stage and constructed a cocoon. A generation is completed in 20 to 28 days. A method of breeding this species on *Ephestia cautella* (Wlk.) is described.

Eiphosoma annulatum Cress. is a solitary endoparasite attacking first- to fourth-stage hosts. The parasites emerge from fifth-stage hosts which may be stunted in size but construct normal cocoons. The life-cycle is completed in 26–35 days.

Bracon thurberiphagae (Mues.) and *Bracon cajani* Mues. are gregarious ectoparasites of similar habit. They paralyse second- to fifth-stage larvae and deposit eggs on or near them. The life-cycle is completed in 13 to 16 days. A method of rearing field-collected immature stages is described.

Perisierola sp. is a gregarious ectoparasite. The adult enters the pod, paralyses a host, and attaches her eggs directly on to the caterpillar. Second- to fifth-stage hosts may be attacked but the larger hosts are preferred. The female frequently remains with her progeny until they have completed their development, which requires 11 to 15 days.

Hyperparasites attacking the parasite pupae are listed.

Details of a shipping container and methods of rearing and shipping parasites to Mauritius for trial against *Etiella zinckenella* (Treitschke) and *Maruca testulalis* (Geyer) are described. From a stock of more than 44,000 cocoons so sent two species, *Bracon cajani* and *Eiphosoma annulatum*, have been successfully established in Mauritius.

Acknowledgements.

Thanks are tendered to Dr. F. J. Simmonds for advice and assistance in preparing the manuscript and to Dr. W. J. Hall for information on the distribution of *Ancylostomia stercorea*. I am also much indebted to Dr. C. F. W. Muesebeck who determined the Braconids and published descriptions of the new species so that the names could be included in the present paper, and to other specialists in the U.S. Department of Agriculture who identified specimens submitted.

References.

Bradley, W. G. (1941). Methods of breeding *Chelonus annulipes* on the Mediterranean flour moth for use against the European corn borer.—*Circ. U.S. Dep. Agric.* no. 616, 22 pp.

Bradley, W. G. & Burgess, E. D. (1934). The biology of *Cremastus flavoorbitalis* (Cameron), an Ichneumonid parasite of the European corn borer.—*Tech. Bull. U.S. Dep. Agric.* no. 441, 15 pp.

Cushman, R. A. (1920). North American Ichneumon-flies, new and described, with taxonomic and nomenclatorial notes.—*Proc. U.S. nat. Mus.* **58** pp. 251–292.

Druce, H. (1896). Biologia Centrali-Americana. Insecta. Lepidoptera-Heterocera **2** p. 284.

Fennah, R. G. (1947). The insect pests of food-crops in the Lesser Antilles.—207 pp. St. George's, Grenada, Deps. Agric. Windw. & Leew. Is.

FULTON, B. B. (1940). The hornworm parasite, *Apanteles congregatus* Say and the hyperparasite, *Hypopteromalus tabacum* (Fitch).—*Ann. ent. Soc. Amer.* **33** pp. 231–244.

GENIEYS, P. (1925). *Habrobracon brevicornis* Wesm.—*Ann. ent. Soc. Amer.* **18** pp. 143–202.

GLOVER, P. M. (1934). The developmental stages of *Bracon tachardiae* Cam. (Hym.).—*Bull. ent. Res.* **25** pp. 521–539.

HEINRICH, C. (1956). American moths of the subfamily Phycitinae.—*Bull. U.S. nat. Mus.* no. 207, 581 pp.

MARTIN, C. H. & FINNEY, G. L. (1946). Factors involved in the separation of *Macrocentrus ancylivorus* cocoons from tuber worm pupae.—*J. econ. Ent.* **39** pp. 29–35.

MOUTIA, L. A. (1957). Considérations sur le complexe biologique des lépidoptères nuisibles à l'embrevadier à Maurice.—*Rev. agric. sucr. Maurice* **36** pp. 256–260.

MUESEBECK, C. F. W. (1925). A revision of the parasitic wasps of the genus *Microbracon* occurring in America north of Mexico.—*Proc. U.S. nat. Mus.* **67** no. 2580, 85 pp.

MUESEBECK, C. F. W. (1955). New reared Braconidae from Trinidad (Hymenoptera).—*Proc. ent. Soc. Wash.* **57** pp. 161–164.

MUESEBECK, C. F. W., KROMBEIN, K. V. & TOWNES, H. K. (1951). Hymenoptera of America north of Mexico: synoptic catalog.—*Agric. Monogr. U.S. Dep. Agric.* no. 2, 1420 pp.

NELSON, W. A. & FARSTAD, C. W. (1953). Biology of *Bracon cephi* (Gahan) (Hymenoptera: Braconidae), an important native parasite of the wheat stem sawfly, *Cephus cinctus* Nort. (Hymenoptera: Cephidae), in western Canada.—*Canad. Ent.* **85** pp. 103–107.

PARKER, D. L. (1935). *Apanteles solitarius* (Ratzeburg), an introduced Braconid parasite of the satin moth.—*Tech. Bull. U.S. Dep. Agric.* no. 477, 17 pp.

PARKER, H. L. (1951). Parasites of the lima-bean pod borer in Europe.—*Tech. Bull. U.S. Dep. Agric.* no. 1036, 28 pp.

ROSENBERG, H. T. (1934). The biology and distribution in France of the larval parasites of *Cydia pomonella*, L.—*Bull. ent. Res.* **25** pp. 201–256.

SHORT, J. R. T. (1952). The morphology of the head of larval Hymenoptera with special reference to the head of the Ichneumonoidea, including a classification of the final instar larvae of the Braconidae.—*Trans. R. ent. Soc. Lond.* **103** pp. 27–84.

SHORT, J. R. T. (1953). A grouping by larval characters of some species of the genus *Apanteles* (Hymenoptera: Braconidae).—*Bull. ent. Res.* **44** pp. 327–332.

SILVESTRI, F. (1923). Contribuzioni alla conoscenza dei Tortricidi delle querce. I.–II.—*Boll. Lab. Zool. Portici* **17** pp. 41–107.

SQUIRE, F. A. (1940). Observations on the larval diapause of the pink bollworm, *Platyedra gossypiella*, Saund.—*Bull. ent. Res.* **30** pp. 475–481.

VANCE, A. M. (1932). The biology and morphology of the Braconid *Chelonus annulipes* Wesm., a parasite of the European corn borer.—*Tech. Bull. U.S. Dep. Agric.* no. 294, 48 pp.

© Commonwealth Agricultural Bureaux, 1959.

STUDIES ON THE BITING HABITS AND MEDICAL IMPORTANCE OF EAST AFRICAN MOSQUITOS IN THE GENUS *AËDES*.

I.—SUBGENERA *AËDIMORPHUS*, *BANKSINELLA* AND *DUNNIUS*.

By A. J. Haddow

The East African Virus Research Institute, Entebbe, Uganda.

During the period 1942–1956 the writer carried out many series of 24-hour catches, to investigate the biting habits of mosquitos and other blood-sucking Diptera in East Africa. The results of some of these investigations have been published (Haddow, 1945*a*, *b*, 1952, 1954, 1956*a*, *b*; Haddow & Dick, 1948; Haddow, Gillett & Highton, 1947; Haddow, Gillett & others, 1950). The greater body of the results has, however, remained unpublished, and in some of the earlier published sections the results were analysed on a 4-hour grouping, which is no longer considered adequate.

In these catches, human bait was used with the single exception of three catches made on monkeys (Haddow & Dick, 1948). Each catch was divided into intervals of one hour or less, and the mosquitos from each period were recorded separately, to permit study of the biting cycle. The methods of catching and the interpretation of the results have been discussed in some detail elsewhere (Haddow, 1954). For the present purpose only the shortest preliminary notes will be given, the series of catches available for discussion being as follows:

(1) The first forest catches. These comprised 15 catches at ground level in the Semliki Forest in Bwamba County, western Uganda (Haddow, 1945*a*).

(2) The Mongiro-Mamirimiri catches. Forty catches were made at these two localities in the Semliki Forest, 20 at each. The Mongiro catches were made simultaneously at ground level, 16, 31 and 54 ft., the highest platform being in the forest canopy. The Mamirimiri catches were made simultaneously at ground level, 22, 44, 58 and 82 ft., the highest platform being in an emergent tree rising above the main canopy (Haddow, Gillett & Highton, 1947).

(3) The Bwamba tree survey. This is the longest series, comprising 240 catches, six at each of 40 stations in the Semliki Forest. In each case catching went on simultaneously at ground level and on a platform in the canopy. The height of the canopy platforms varied with the type of forest from 36 to 77 ft., with a mean of 54 ft.

(4) The Entebbe tree survey. In this series there were 35 catches, five at each of seven stations. One of these stations was in lake-shore forest at Kitinda; all the others were in forest fringing the extensive papyrus swamp at Zika. In this work, catching proceeded simultaneously at ground level, in the understorey and in the canopy. The heights of the understorey platforms varied from 27 to 38 ft. (mean 35 ft.) and those of the canopy platforms from 52 to 65 ft. (mean 58 ft.).

(5) The Zika canopy series. This comprised 60 weekly catches on the Zika No. 4 canopy platform (65 ft.). In this series the arrival of the mosquito on the bait was recorded to the nearest minute. A small section of this series has been discussed elsewhere (Haddow, 1956*b*).

(6) Five catches in riverside thicket at Loyoro, Karamoja. This is very dry country. The catches were made on a platform at 15 ft., well up in the thicket.

(7) Six catches in mangrove (*Avicennia marina*) at Penda Kula, Mida Creek, Kenya coast. As the spring tides wash through the *Avicennia*, these catches were carried out on a platform raised a little above the mud.

(8) The first plantation catches. This series consisted of 15 catches at ground level in banana plantations round the edges of the Semliki Forest (Haddow, 1945*a*).

(9) The stratified plantation catches. Ten catches were made in a banana plantation in Bwamba, catching going on simultaneously at ground level and on platforms 6, 12 and 18 ft. above ground (Haddow, 1945*b*).

(10) Five catches at ground level in a banana plantation contiguous with Zika Forest.

(11) Five catches in a hut 80 yd. from the edge of Zika Forest and one catch in a hut at Hakitengya, Bwamba.

(12) Two catches made in the canopy of the Semliki Forest with anaesthetised monkeys as bait. One similar catch in Zika Forest, carried out simultaneously at ground level, 34 and 52 ft. (Haddow & Dick, 1948).

The total number of catches available for discussion is thus 440. The sample of mosquitos is over 117,000 and the number of species is over 80. The Tabanids taken in this work have been discussed previously (Haddow, Gillett & others, 1950; Haddow, 1952) as have the mosquitos of the genus *Eretmapodites* (Haddow, 1956*a*).

During the earlier part of the work, local mean time was the measure employed. Later, the more accurate method introduced by Lumsden (1952) was employed, 1800 hr. catch time always being equated to the exact time of sunset. With the exception of the catches at Penda Kula (between 3° and 4° south) and those at Loyoro (between 3° and 4° north) the entire work was carried out within 1° of the equator. Thus night and day were of approximately equal duration throughout the year.

In analysing the results of long series of catches, use has been made of the measure described in an earlier paper (Haddow, 1954) as "the geometric mean as modified by C. B. Williams," for which the term "Williams' mean" (M_w) is now proposed (see Appendix, p. 779).

In the forest series, the highest level reached was the main canopy, with the single exception of the 82-ft. platform at Mamirimiri, which was in an emergent tree. While it is hoped to begin work above the canopy in the near future, practically nothing is known about this zone at present.

At a fairly early stage in the work the first stratified catches in forest were carried out, and it at once became apparent that while certain mosquitos are predominantly ground-haunting, others are essentially arboreal. In some cases, such as the genus *Aëdes*, this generalisation can be extended to subgenera (Haddow, Gillett & Highton, 1947). The present paper is concerned with the subgenera which are essentially ground-haunting, namely, *Aëdimorphus*, *Banksinella* and *Dunnius*. The writer's figures for the subgenera *Ochlerotatus* and *Skusea* are inadequate for discussion and the results for the subgenera *Mucidus*, *Finlaya* and *Stegomyia*, which include at least some markedly arboreal members, will be presented separately.

The biting behaviour found in members of the three subgenera will now be discussed, after which an appraisal of the potential medical importance of the mosquitos concerned will be given.

The Subgenus *Aëdimorphus*.

A very large number of species in this subgenus occurs in Africa, and members fall into a number of relatively well-defined groups. Edwards (1941) lists nine such, and these will be followed here. The *ochraceus* (Theo.) group of Edwards was not represented, and in the *lamborni* group (the only member of which is *A.* (*A.*) *lamborni* Edw.) only five specimens were taken. These occurred in the Mongiro-Mamirimiri catches. All were taken at ground level, four by day and

one in the hour after sunset. The remaining groups may now be discussed in more detail.

Edwards' first three groups (the *apicoannulatus* (Edw.), *argenteopunctatus* (Theo.) and *domesticus* (Theo.) groups) may be considered together. The members are small sylvan mosquitos, most of them warm brown in colour and with distinct and characteristic silver markings. The members of the first two groups are, in fact, rather reminiscent of the subgenus *Stegomyia* in general appearance. These mosquitos are never taken in large numbers in catches made with human bait but in some forest areas many may be found resting in the undergrowth. It seems unlikely that man is the preferred host. The numbers, even in the long series of catches here discussed, are inadequate for detailed analysis. The arithmetic totals for catches of species in these three groups made at ground level in forest, together with those for three species in other groups, are given in Table I, which includes all the less abundant species.

TABLE I.

The biting cycles of the less abundant species.

Hour	*A. (A.) capensis*	*A. (A.) stokesi*	*A. (A.) haworthi*	*A. (A.) simulans*	*A. (A.) argenteo-punctatus*	*A. (A.) mutilus*	*A. (A.) domesticus*	*A. (A.) leptolabis*	*A. (A.) natronius*	*A. (B.) albothorax*	*A. (D.) albomar-ginatus*
00–01	1	—	—	1	1	1	3	—	1	—	—
01–02	1	—	—	—	—	2	1	—	—	1	—
02–03	—	1	—	—	2	—	2	—	3	—	—
03–04	—	1	—	—	—	2	1	—	—	—	1
04–05	—	—	—	—	—	2	3	—	—	—	—
05–06	—	—	—	—	—	1	2	—	—	1	1
06–07	—	—	—	—	1	2	5	1	—	1	—
07–08	1	4	—	—	2	3	4	1	—	4	—
08–09	1	5	2	1	—	5	6	1	—	3	—
09–10	—	—	—	2	2	4	1	2	—	3	3
10–11	—	3	—	1	—	4	6	2	—	4	2
11–12	1	1	—	1	3	3	2	1	—	3	3
12–13	—	4	—	—	1	4	2	—	—	—	3
13–14	—	1	—	1	4	2	5	2	—	3	4
14–15	—	1	—	—	3	—	5	1	—	2	4
15–16	—	2	—	—	4	1	2	—	—	3	6
16–17	—	5	—	2	2	—	4	2	—	—	7
17–18	—	2	—	3	3	1	3	4	1	2	2
18–19	—	1	—	1	3	1	6	—	8	—	2
19–20	—	1	—	1	3	—	3	—	13	—	—
20–21	—	—	—	—	1	2	2	—	3	—	1
21–22	2	—	—	1	—	1	3	—	1	—	—
22–23	—	—	—	—	1	3	1	—	—	1	—
23–24	—	—	—	—	—	—	1	—	1	—	—
Totals	7	32	2	15	36	44	73	17	31	31	39

The figures show the numbers taken at ground level in forest, with the exception of *A. natronius*, where they refer to the numbers taken on tree platforms in forest. In this table a dash indicates that no specimens were obtained.

A. (*A.*) *capensis* Edw. was encountered only in Bwamba County and only at ground level during the 24-hr. catches, but survey work has shown that it is present also in the Itwara, Kibale and Mabira Forests, Uganda. The seven specimens obtained were all taken in forest, but the evidence of mass catches has shown that this species also occurs in banana plantations.

A. (*A.*) *stokesi* Evans was also rare. In the work under discussion it was taken in forest only, but mass catches have shown, as in the case of the preceding species, that it may occur in banana plantations. There have been records of *A. stokesi* from the forest canopy, but in the present work (with the single exception of a specimen taken on a low (16-ft.) platform at Mongiro) it was taken at ground level only. Altogether, 32 specimens were obtained in 24-hr. catches, all in the Semliki Forest, and of these, 28 (88%) were obtained by day. The biting cycle, apart from its broadly diurnal nature, showed no clear features. All that can be said at the moment is that this is a rare diurnal mosquito of the forest floor.

A. (*A.*) *haworthi* Edw. has been taken by the writer only in the Entebbe area, in forest. Early records of *A. haworthi* from Bwamba (Haddow, Gillett & Highton, 1947) should be referred to the next-mentioned species. The two specimens so far taken in 24-hr. catches were both obtained by day.

In East Africa, *A.* (*A.*) *simulans* (Newst. & Cart.) appears to be confined to the Bwamba lowlands and Bugoma Forest, Uganda. Fifteen specimens were taken in the Bwamba tree survey, all at ground level. Of these, 11 were taken by day, and the evidence of mass catches in forest likewise suggests that this is a diurnal mosquito. It has occasionally been taken in banana plantations.

A. (*A.*) *argenteopunctatus* (Theo.) is not uncommon in some types of second-growth forest (that is, forest that has regenerated after felling) and can sometimes be taken in fair numbers in the undergrowth. It is not, however, common in 24-hr. catches. This is essentially a mosquito of the forest floor though it also occurs in plantations. In the Bwamba tree survey, 35 were taken at ground level and nine in the canopy, but these nine occurred in three individual catches, and only two of the 40 stations were involved. It is interesting to note that while at ground level in forest this mosquito is essentially diurnal, all the canopy specimens occurred by night, as did two taken in 24-hr. catches in banana plantations. A total of 36 was taken at ground level in forest—one in the first forest catches and the remainder in the Bwamba tree survey. Of these, 25 (69%) were obtained by day. Apart from this broadly diurnal nature, the cycle was ill-defined, though there is an indication of a possible preference for the afternoon.

A. (*A.*) *mutilus* Edw. was taken in Bwamba only, and all the specimens obtained by 24-hr. catching came from forest, though mass catches have shown, as in the case of other species, that it sometimes enters plantations. Like the others of Edwards' first three groups it is essentially a mosquito of the forest floor. In the 240 catches of the Bwamba tree survey, for example, 41 were taken at ground level, and only five in the canopy. The total ground-level sample is 44, three having been taken in earlier series. Of these, 29 (66%) were taken by day, mainly in the morning. As in the preceding species, those taken in the canopy were all obtained by night.

A. (*A.*) *domesticus* (Theo.) was encountered only in Bwamba, at ground level in forest, although it does occur in plantations. In the first forest catches, nine were taken, in the Mongiro-Mamirimiri series one other was obtained and in the Bwamba tree survey 63. The biting cycle, as shown by this sample of 73, is without marked characteristics. Biting was somewhat more active by day, when 45 specimens (62 per cent. of the total) were obtained.

A. (*A.*) *leptolabis* Edw. is a very close relative of *A. domesticus*. So far it has been encountered only in the Entebbe area, at ground level in forest by night, but only 17 examples have been taken.

It may be noted that in the case of *A. domesticus* and *A. leptolabis* the identification has been based on the examination of male terminalia. All the males so far taken by the writer in Bwamba have proved to be *A. domesticus* and all those in the Entebbe area *A. leptolabis*. It is not considered that identification based on the external features of the females is reliable.

When the figures for the various species of Edwards' first three groups are considered as a whole, it is found that 243 were taken, of which 241 were obtained in forest and only two in plantations. Of the forest specimens, 226 (94%) occurred at ground level. When the biting cycle in forest is examined, it is found that at ground level it is essentially diurnal, 160 (71%) having been obtained by day. On the other hand, of the 15 specimens taken on tree platforms, 14 were obtained by night, and the specimen which was obtained by day was not taken in the canopy but on a low (16 ft.) platform where conditions did not differ greatly from those at ground level (Haddow, Gillett & Highton, 1947). The members of these groups may thus be characterised as somewhat scarce diurnal mosquitos of the forest floor, whose biting habits tend to become nocturnal in the case of the few specimens which visit the canopy. The same may be true of those taken in banana plantations, though the numbers here are inadequate for discussion.

TABLE II.

The biting cycles of the more abundant species at ground level, in forest.

Hour	*A.* (*A.*) *tarsalis* group		*A.* (*A.*) *abnormalis* group		*A.* (*A.*) *cumminsi*		*A.* (*B.*) *circumluteolus*		*A.* (*B.*) *palpalis*	
	No. taken	M_G × 100	No. taken	M_G × 100	No. taken	M_G × 100	No. taken	M_G × 100	No. taken	M_G × 100
00–01	13	3	15	4	107	18	55	8	23	4
01–02	7	2	10	3	122	19	69	9	30	5
02–03	7	2	6	2	93	16	39	5	43	7
03–04	18	4	9	3	84	16	58	7	34	6
04–05	11	2	3	1	86	14	43	6	51	6
05–06	29	7	10	3	106	16	40	7	41	6
06–07	63	12	25	7	122	24	85	14	69	13
07–08	66	14	16	5	98	20	99	16	84	14
08–09	75	15	27	8	117	25	110	19	85	16
09–10	61	13	16	4	112	23	133	21	111	19
10–11	63	13	16	4	121	24	121	21	95	18
11–12	38	8	17	5	121	26	114	19	76	15
12–13	32	7	13	4	113	22	141	20	109	21
13–14	34	7	12	3	129	25	143	21	95	15
14–15	36	9	14	4	136	27	140	19	94	18
15–16	38	8	19	5	141	25	166	24	111	20
16–17	46	10	13	4	180	29	165	25	59	13
17–18	89	18	37	10	256	47	149	23	67	13
18–19	68	13	29	8	279	50	89	13	51	10
19–20	31	7	25	6	190	37	74	9	43	6
20–21	15	4	12	4	139	24	70	10	37	6
21–22	11	2	11	3	142	25	59	9	40	6
22–23	16	4	7	2	96	18	34	6	34	5
23–24	13	3	8	2	127	24	42	7	41	6
Totals	880	—	370	—	3217	—	2238	—	1523	—

The geometric means (M_G) have been multiplied by 100 to give integer numbers for the sake of compactness in tabulation.

The next group of *Aëdimorphus* to be considered—the *tarsalis* (Newst.) group of Edwards—is an important one, whose members are abundant in most of the equatorial forest of Africa. They are taken most easily by collecting on the undergrowth or by the use of moving baits, but fairly large numbers also occurred in the 24-hr. catches.

At Entebbe, *A.* (*A.*) *tarsalis* (Newst.) is the only member of the group so far encountered, but in Bwamba there are three others in addition: *A.* (*A.*) *phyllolabis* Edw., *A.* (*A.*) *albocephalus* (Theo.) and *A.* (*A.*) *smithburni* van Som. These, however, seem to be relatively uncommon, and it is believed that probably over 90 per cent. of the Bwamba specimens discussed below are *A. tarsalis, sensu stricto*. The females in the *A. tarsalis* group are not reliably distinguishable, and this view is based on the dissection of wild-caught males and of males bred in captivity.

As *A. tarsalis* is essentially a mosquito of the heavier forest, it is not prevalent in the light patchy forest of the Entebbe area. In the 35 catches of the Entebbe tree survey only nine were taken, six by day and three by night, all at ground level. These need not be discussed further. In the case of the forest catches in Bwamba the original series yielded 93, the Mongiro-Mamirimiri series 226 and the Bwamba tree survey 561 at ground level. As the results show similar trends, these series may be combined to give a total sample of 880, the results being given in Table II and fig. 1.

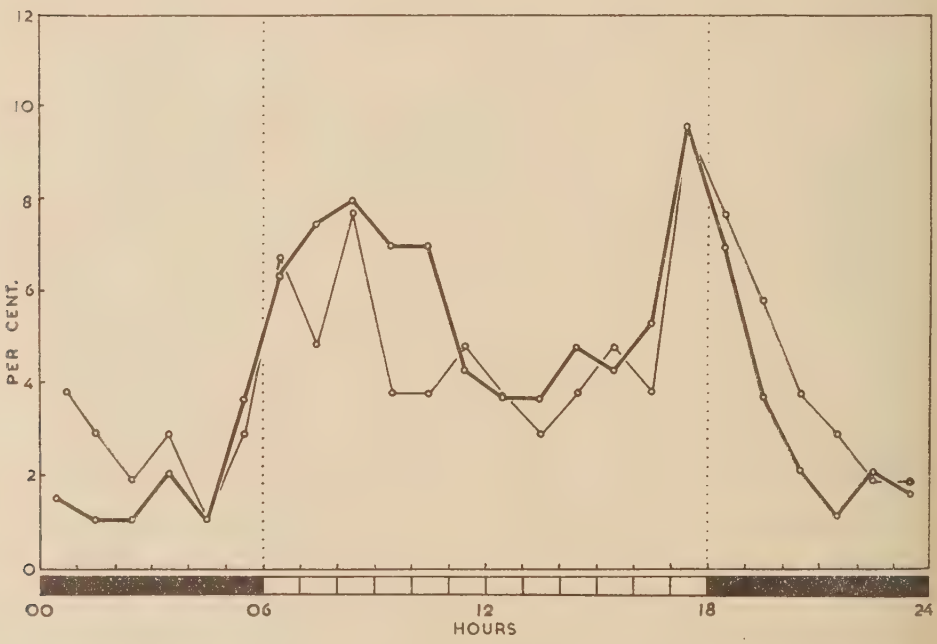


Fig. 1.—The biting cycle of the *A. tarsalis* group (thick line) and *A. abnormalis* group (thin line) at ground level in forest. The figures are geometric means (M_G) reduced to percentages to facilitate comparison.

The form of the biting cycle as shown in the original paper on the Mongiro-Mamirimiri catches (Haddow, Gillett & Highton, 1947) seems different from those for the other two forest series, but analysis shows that this is merely due to the fact that a 4-hr. grouping was employed. On a 1-hr. basis all the figures show

the same trend. The biting cycle is essentially diurnal, with a markedly biphasic nature, one major wave of activity occurring in the morning, and the other in the late afternoon. This type of cycle has been noted in the case of various other forest species and was first observed by Kumm & Novis (1938) in South American mosquitos.

The group is essentially ground-haunting. Thus, of the 249 taken in the Mongiro-Mamirimiri series, 226 (91%) were obtained at ground level, and only 23 in the trees. All of the latter were taken on the lower platforms, well below the canopy, and the biting cycle was diurnal, as at ground level, 20 of the 23 being taken by day. There is, however, an indication that on the rare occasions when *A. tarsalis* does bite in the canopy it tends to be nocturnal. Thus, of the 569 taken in the 240 catches of the Bwamba tree survey, only 8 specimens (1%) were taken in the canopy, but, of these, 7 were obtained by night. This is reminiscent of some results discussed above, in certain species of Edwards' first three groups.

Being essentially a mosquito of the forest floor, *A. tarsalis* is seldom abundant in banana plantations, though fair numbers may sometimes be taken there by catching on the undergrowth or by using moving baits. During the various series of 24-hr. catches made in Bwamba, however, only one specimen was taken in plantations.

The *abnormalis* (Theo.) group of Edwards is closely allied to the *tarsalis* group, and once again the females are not reliably distinguishable. So far the group has been encountered mainly in Bwamba County, though a few specimens have been taken at Entebbe. Mass catches have shown that it may occur in plantations, but in 24-hr. catches it was taken in forest only. The species known to occur in Bwamba are *A.* (*A.*) *abnormalis* ssp. *kabwachensis* Edw., *A.* (*A.*) *congolensis* Edw., *A.* (*A.*) *tricholabis* ssp. *bwamba* van Som., *A.* (*A.*) *semlikiensis* van Som. and *A.* (*A.*) *wigglesworthi* Edw. Of these, only the first is common and it probably comprises over 90 per cent. of the sample here discussed. Very few specimens taken in 24-hr. catches prior to the Bwamba tree survey could be definitely identified as belonging to this group. This particular series of catches, to which, therefore, the discussion will be confined, yielded 381 specimens, of which 370 (97%) were taken at ground level, and only 11 in the canopy. At ground level the biting cycle closely resembled that of *A. tarsalis*, being essentially diurnal and biphasic, as shown in Table II and fig. 1. In the canopy, as in the case of various species discussed above, biting activity was mainly nocturnal, 10 of the 11 specimens having been taken at night.

Between the closely allied *tarsalis* and *abnormalis* groups (which Edwards distinguished on morphological characters) there is thus also a close similarity where one type of cyclical behaviour, biting activity, is concerned. That this suggestion of a group behaviour pattern is not, however, universally applicable is shown by the work of Mattingly (1949) in West Africa. In his catches, two members of the *abnormalis* group, *A.* (*A.*) *irritans* (Theo.) and *A.* (*A.*) *nigricephalus* (Theo.), were well represented. *A. irritans* conformed to the above pattern, showing a strikingly biphasic biting cycle with the peaks just after sunrise and just before sunset, but *A. nigricephalus* differed completely, having a rather ill-defined cycle, which was none the less essentially nocturnal, 71 per cent. of the total catch having been obtained by night. However, *A. nigricephalus* differs strikingly in appearance and in the structure of the male terminalia from all other members of the *abnormalis* and *tarsalis* groups, and it seems possible that it should stand alone, or be assigned to another group.

Where vertical distribution was concerned, Mattingly's results for these two species show clearly that, like other members of the *abnormalis* group, they have a marked preference for ground level. His 24-hr. catches were carried out simultaneously at ground level, 22, 40 and 52 ft. In *A. nigricephalus*, 87 per

cent. of the total sample was taken at ground level, and in *A. irritans*, 89 per cent.

The next group, the *dentatus* (Theo.) group, is a large one, but many of the East African species are inhabitants of the higher country and so were not represented in the catches here discussed. *A.* (*A.*) *dentatus* (Theo.) appears to bite mainly at sunset and dawn (J. D. Gillett, private communication). Apart from a rare unidentified species resembling *A. dentatus* but probably distinct, which has been taken in trifling numbers in Bwamba and at Entebbe, the only member of the group represented in the 24-hr. catches was *A.* (*A.*) *cumminsi* (Theo.). Two subspecies, *holocinctus* Edw. and *mediopunctatus* (Theo.), occur in Bwamba, as well as the typical form, but they are not treated separately here, as intergrades seem to occur.

A. cumminsi appears to be primarily a forest mosquito, but it occurs also in all kinds of second-growth forest and heavy bush, and also in banana plantations. It may also enter huts, two having been taken by the writer in a hut by night in Bwamba, during a 24-hr. catch, and one by Lumsden (1951) during a similar catch in the same area. Lumsden also took *A. cumminsi* biting in the cleared space around huts. At Entebbe it is relatively scarce and during the Entebbe tree survey only five were taken, all at ground level, four by day and one by night. These need not be discussed further.

In Bwamba, large numbers were taken at ground level in forest during 24-hr. catches. Of these, 542 were obtained in the first forest catches, 45 during the Mongiro-Mamirimiri series and 2,630 in the Bwamba tree survey. These series may conveniently be combined to give a total sample of 3,217 (Table II & fig. 2).

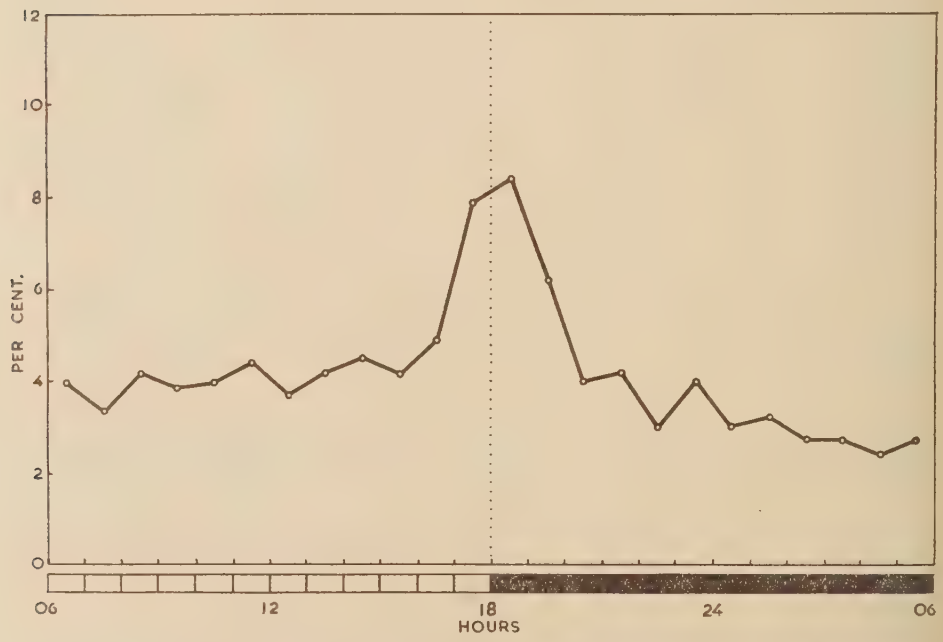


Fig. 2.—The biting cycle of *A. cumminsi* at ground level in forest. The figures are geometric means (M_G) reduced to percentages to facilitate comparison with other species.

The biting cycle is clearly defined. Some activity goes on throughout the 24 hours, but there is a single pronounced peak covering the hour before and the hour after sunset.

Like most other members of the subgenus, *A. cumminsi* is scarce in the trees and only 28 were taken on tree platforms, four in the Mongiro-Mamirimiri series and 24 in the Bwamba tree survey. As in the case of some species discussed above, the biting cycle differed from that at ground level. No clearly defined peak of activity was shown, but 24 of the 28 specimens (86%) were taken by night. In banana plantations also the cycle was mainly nocturnal. Thus of 71 taken in the first plantation catches 64 (90%) were obtained by night. In plantations, however, the crepuscular peak of activity was clearly apparent, though here it was confined to the single hour after sunset, when 12 specimens (17 per cent. of the total catch) were obtained. The results of J. D. Gillett's 24-hr. catches of *A. cumminsi* in banana plantations correspond closely to those just discussed. Thus 25 of a total of 34 (74%) were taken by night, and again there was a striking peak of activity in the single hour after sunset, when 12 specimens (35 per cent. of the total) were obtained (personal communication).

Where vertical distribution is concerned, it is clear that *A. cumminsi* is strictly a ground-haunting mosquito. Thus, in the Mongiro-Mamirimiri catches, 45 were taken at the two ground-level stations, and only four on the seven platforms. In the Bwamba tree survey the results were even more striking, as here 2,654 were obtained, of which 2,630 (99%) were taken at ground level. It is interesting also to note how regular was the occurrence of this species at ground level in forest. Thus in the Bwamba tree survey it was taken at all 40 stations, and it was present in 185 of the 240 catches.

The last member of the subgenus *Aëdimorphus* to be considered is *A.* (*A.*) *natronius* Edw., which Edwards assigns to the *vexans* (Mg.) group. In the work

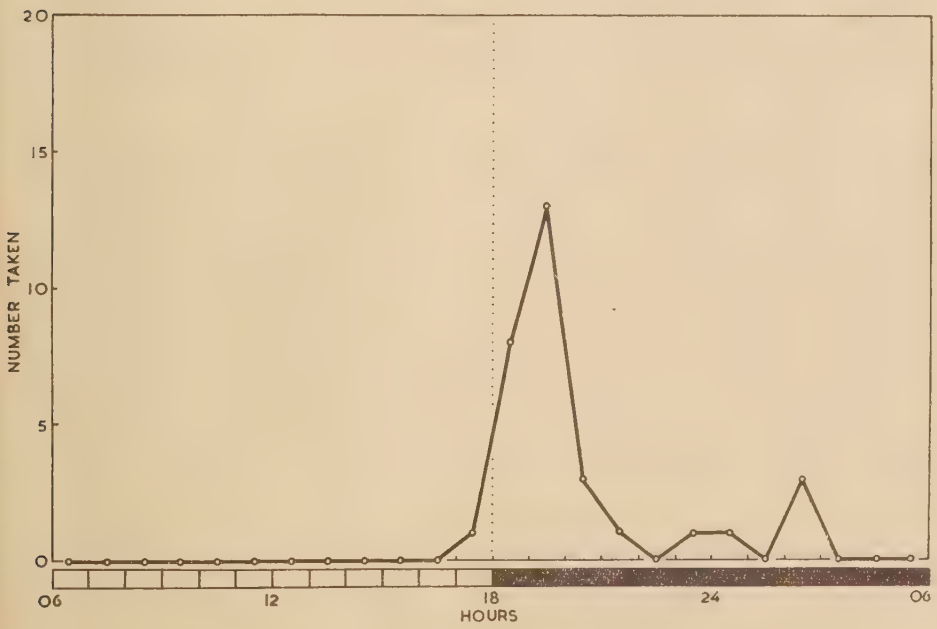


Fig. 3.—The biting cycle for *A. natronius* on tree platforms. Arithmetic totals are given as the figures are too small for detailed analysis.

here considered, *A. natronius* was taken only in the Mongiro-Mamirimiri area, which adjoins the hot saline springs of Mbuga and Nyansimbi. It is not common even in this area. During the Bwamba tree survey only one specimen was taken (at 20–21 hr., in the canopy) and the discussion will here be confined to the 42 specimens taken during the Mongiro-Mamirimiri catches of 1944–45.

Unlike the other species of *Aëdimorphus* here discussed, *A. natronius* has distinct arboreal tendencies, at least in forest areas. Thus 28 specimens (67 per cent. of the total) were taken at heights over 40 ft. and 18 (43%) actually in the canopy.

The next point of interest concerns the biting cycle. Of 11 specimens taken at ground level, five were obtained by day and six by night. Of the 31 specimens taken on tree platforms, however, all but one were taken by night, and the single exception occurred in the hour before sunset. Though the sample is very small, the biting cycle in the trees is clearly defined, with a sharp peak of activity in the second hour after sunset (Table I & fig. 3) when 13 specimens (42 per cent. of the total) were obtained.

In the 3-hr. period after sunset 24 (77 per cent. of the total) were taken. The differences between *A. natronius* and other members of the subgenus are thus rather striking, and it would be interesting to carry out further studies in an area where it is more prevalent.

The Subgenus *Banksinella.*

Though the members of this subgenus have for long been recognised as ' nuisance mosquitos ', it is only within the past few years that any have been incriminated as vectors of disease. This will be discussed further below. For the moment it is enough to note that one very common species, *A.* (*B.*) *circumluteolus* (Theo.) has proved to be one of the most important virus vectors of Africa, and that other species also may be involved.

A. (*B.*) *lineatopennis* (Ludl.) is common in Kenya, where the writer met it frequently as a day-time biting species, common out of doors, and occasional in huts (Haddow, 1942), but in the present catches it did not occur, being scarce and local in Uganda.

A. (*B.*) *circumluteolus* (Theo.) was the most prevalent member of the subgenus in the work under discussion, occurring in almost all the series of catches. Very common in catches made with moving baits, it tends to be less well represented in 24-hr. work where the baits are stationary—a fact also noted by De Meillon, Paterson & Muspratt (1957). It bites freely in bush, forest and plantations and in the open. Its scarcity in huts is clearly shown by Lumsden's 24-hr. catches carried out simultaneously in various environments (1951) and by the fact that De Meillon and his co-workers failed to find it in huts in an area where almost 5,000 were taken in other environments. The latter workers have shown that this mosquito feeds in nature on cattle, goats and dogs as well as on man. They found it most prevalent in bush and scrub, but forest appears to be the preferred habitat in Uganda.

At ground level in forest, *A. circumluteolus* bites throughout the 24 hours, but is most active by day, as is shown by the following summary:

	No. taken	No. taken by day	
First forest catches	49	33	
Mongiro-Mamirimiri catches	156	110	
Bwamba tree survey	1998	1389	
Entebbe tree survey	35	34	
Total	2238	1566	(70%)

Its prevalence in this habitat is shown by the fact that it was taken in 200 of the 330 catches listed above and at 44 of the 50 localities concerned.

The results of all the ground-level series in forest being very similar, it seems permissible to combine them in order to show the biting cycle as observed in this environment (Table II & fig. 4). The cycle is markedly diurnal, but does not

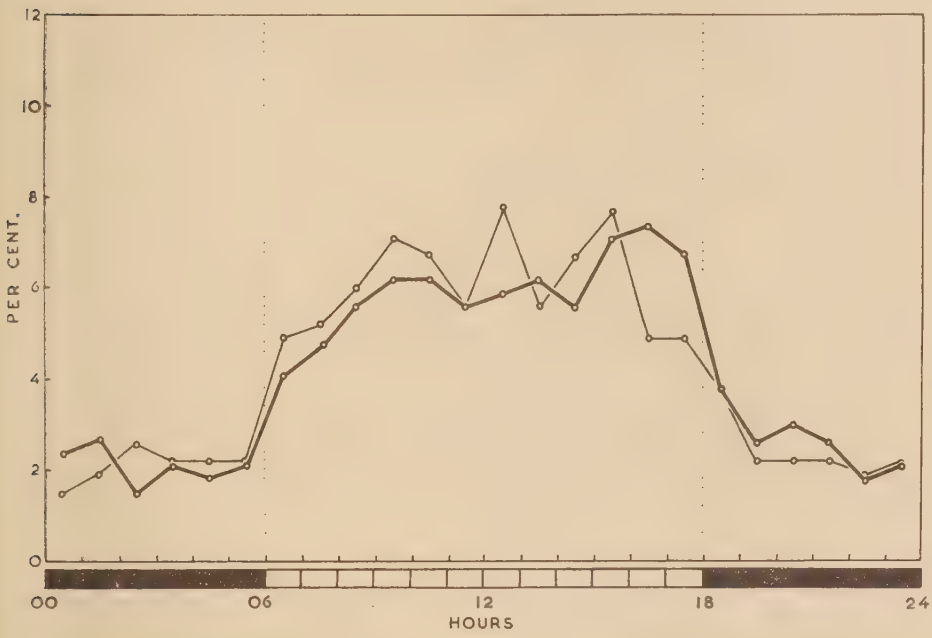


Fig. 4.—The biting cycle of *A. circumluteolus* (thick line) and *A. palpalis* (thin line) at ground level in forest. The figures are geometric means (M_G) reduced to percentages to facilitate comparison.

show any very striking characteristics apart from a general trend upwards to a maximum in the late afternoon. Working in West Africa, Mattingly (1949) found in a smaller sample that the cycle was diurnal there also, but the afternoon peak was much more clearly marked in his catches, and there was also a tendency towards a lesser peak in the morning.

In the case of certain other mosquitos (*A.* (*Finlaya*) *longipalpis* (Grünb.) and *Eretmapodites* spp.) and of the arboreal Tabanid, *Chrysops centurionis* Aust., it has been shown that apparently simple cycles may be broken up into a number of more complex components (Haddow, 1952, 1954, 1956*a*). Analysis on these and other lines has not, however, succeeded in the case of *A. circumluteolus* and all that may be said is that the cycle is essentially diurnal, varying somewhat from catch to catch, and with a general tendency toward heightened activity in the late afternoon.

Once again there is a tendency for the cycle to be altered in different environments. In the Mongiro-Mamirimiri catches, a few specimens were taken on low platforms (under 30 ft.) and at these levels the cycle was still definitely diurnal, eight of the nine obtained having been taken by day. On high platforms, particularly in the canopy, however, the cycle was nocturnal. Thus in the case of three taken in the Mongiro-Mamirimiri catches at heights of over 30 ft., 27

taken in the canopy in the Bwamba tree survey, four taken on platforms at heights of over 30 ft. in the Entebbe tree survey, and 18 taken at 65 ft. in the long series of catches at Zika No. 4 station (total 52 mosquitos), biting was mainly nocturnal, 34 specimens (65 per cent. of the total) having been taken by night. This result would have been still more striking but for the fact that, in a single freak catch, nine were taken by day—this figure representing half the total taken by day on high platforms.

A similar trend towards nocturnal biting was shown in plantations. Thus of 13 taken in the original plantation catches, 12 were obtained by night.

It is interesting to compare these results with figures obtained by Lumsden (1951) in 24-hr. catches made simultaneously in different environments. His results were:

Forest canopy	0
Forest floor	260
Banana plantations	55
Open space between hut, forest and plantation	79
Inside hut	2

Lumsden has not published the detailed hourly figures for these catches, but has shown the results divided according to whether or not the particular habitat is likely to be inhabited by man at the time concerned. It may be deduced, however, that, in forest, biting was most active by day (260 bit between 05 and 19 hr. and 76 between 19 and 05 hr.). In the plantation the situation was entirely different, as 27 bit between 05 and 19 hr., and 28 between 19 and 05 hr. (it should be remembered that the first group includes the catch for two hours of darkness). In the open ground, while at first sight biting seems to have occurred mainly by day (72 of 79 bit in the period 05–20 hr.), it would be interesting to know how many were taken in the three hours of darkness here included.

The fact that *A. circumlutcolus* is a ground-haunting species is clearly brought out by all the series of stratified catches here discussed. In the Mongiro-Mamirimiri series, 156 were taken at the two ground-level stations and only 12 on the seven platforms placed at various heights in the trees. In the Bwamba tree survey, 1,998 were taken at ground level and only 27 in the trees (a ratio of 74:1). In the Entebbe tree survey, 35 were taken at ground level, two in the under-storey and two in the canopy. Lumsden's catches, referred to above, yielded 260 on the forest floor and none in the canopy. This situation holds good in West Africa also, as Mattingly (1949) obtained 90·3 per cent. of his total catch at ground level, 8·7 per cent. at 22 ft., 1·0 per cent. at 40 ft., and nothing at 52 ft. Thus, like most of the other species here discussed, *A. circumluteolus* appears as a diurnal mosquito of the forest floor, though the biting cycle may in other environments tend to become nocturnal.

A. (*B.*) *palpalis* (Newst.) has not so far been obtained in the Entebbe area, though the writer has taken it at Sango Bay and it is known to occur near Kampala (Edwards, 1941). In Bwamba it is very largely confined to forest. Thus in the first series of 15 catches in forest, 189 were taken, while in the corresponding plantation series only three were obtained. In the later series of ten stratified catches in plantations, *A. palpalis* did not occur.

Good samples were obtained in the first forest catches, which yielded 189, and the Bwamba tree survey, which yielded 1,334 at ground level. The results of these two series, which showed similar trends, have been combined to show the biting cycle (Table II & fig. 4). As only one was obtained in the Mongiro-Mamirimiri catches, this series need not be considered. The cycle is, like that of *A. circumlutcolus*, essentially diurnal, 1,055 specimens (69 per cent. of the total) having been taken by day. It is, however, more irregular, and it lacks

the rise in activity during the late afternoon which appears to be characteristic of *A. circumluteolus*. The specimens taken in the canopy and in banana plantations are too few for discussion of the cycle in these environments.

Like *A. circumluteolus*, this mosquito is a markedly ground-haunting species. Thus in the Bwamba tree survey it was taken in 94 catches at ground level, while in the canopy it occurred in five catches only. As opposed to 1,334 specimens taken at ground level, the yield from the canopy was only seven.

Two other species of *Banksinella* were encountered in Bwamba. One, *A.* (*B.*) *taeniarostris* (Theo.), is a rare forest species, which occasionally enters plantations. In 24-hr. catches, only two were taken, both in forest and both at ground level. The evidence of mass catches suggests that, like the two species just discussed, it is essentially diurnal. The other, *A.* (*B.*) *albothorax* (Theo.), is not uncommon in mass catches in forest and plantations, but in the case of 24-hr. work it was encountered only during the Bwamba tree survey, at ground level. The numbers are small, but show adequately that this is another diurnal species as, of a total of 31, 28 were taken by day (Table I).

An uncommon species encountered by Mattingly (1949) is *A.* (*B.*) *punctocostalis* (Theo.). Only six specimens were obtained in his catches, but, of those, five were taken by day. All came from ground level.

Thus all the members of this subgenus so far studied are predominantly ground-haunting mosquitos whose main biting activity occurs by day.

The Subgenus *Dunnius*.

Only one member of this subgenus, *A.* (*D.*) *albomarginatus* (Newst.), was encountered. All the specimens came from Bwamba and were taken at ground

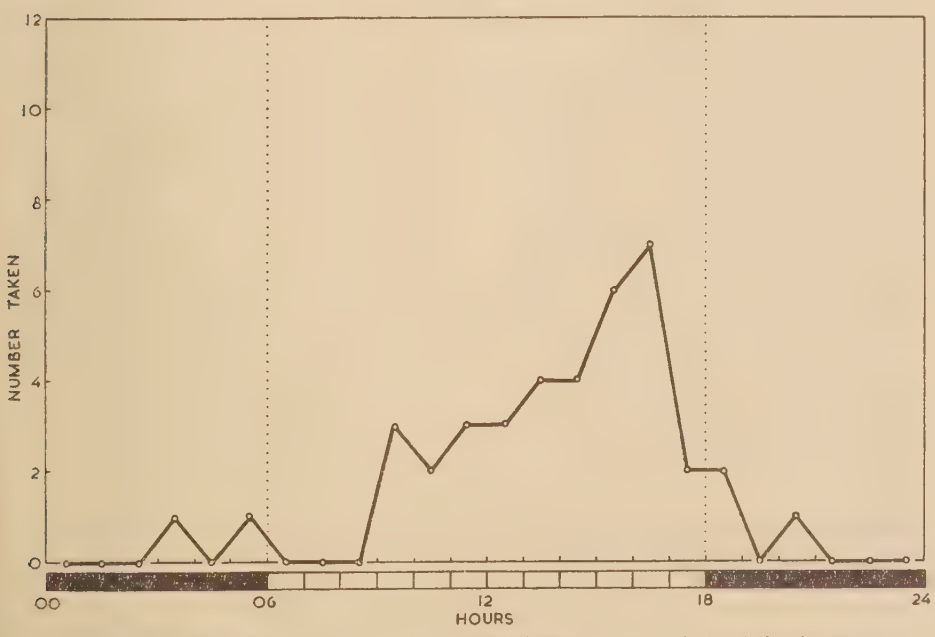


Fig. 5.—The biting cycle of *A. albomarginatus* at ground level in forest. Arithmetic totals are given as the figures are too small for detailed analysis.

level. Mass catches have shown that it does occur in plantations, but in 24-hr. work it was taken only in forest. In the original forest catches, three were obtained, and a further 36 were taken in the Bwamba tree survey. Though the number is very small, the biting cycle is clear-cut, being diurnal, with a well-marked peak in the late afternoon (Table I & fig. 5). Of the 39 specimens obtained, 34 were taken by day, and 21 in the period 13–17 hr.

The Medical Importance of the three Subgenera.

Over a period of years, members of this Institute have been engaged in an extensive programme concerned with the isolation of yellow fever virus from wild mosquitos, mainly in Bwamba County and the Entebbe area. During this work, several other viruses have been isolated, and, in some of these isolations, members of the three subgenera here discussed were involved. In the case of these viruses, subsequent surveys of immunity in man have shown in every case that infection occurs over very wide areas in Africa and, in some cases, in other continents as well. To save repetition of references, the main papers on this survey work will be listed at this stage as follows: East Africa—Smithburn (1952); Egypt—Smithburn, Taylor & others (1954); South Africa—Kokernot, Smithburn & Weinbren (1956); India—Smithburn, Kerr & Gatne (1954); Malaya and Borneo—Smithburn (1954); Singapore and Borneo—Hale, Lim & Lee (1956); Brazil—Causey & Theiler (1958).

In 1942, Semliki Forest virus was first isolated from a lot of 130 examples of the *A. abnormalis* group caught at Budinyama, in a gallery extension of the Semliki Forest (Smithburn & Haddow, 1944). The only subsequent isolation was made in West Africa from a mosquito of an entirely different group, *Eretmapodites grahami* Edw. (MacNamara, 1953). It is known in addition that, even in Bwamba, the *A. abnormalis* group cannot be the only vectors as, after the isolation, it was found that two laboratory monkeys that had been inoculated with other groups of Bwamba mosquitos had also become immune. As, however, they had shown no overt sign of illness, it was not possible to tell which groups had been involved. One of these monkeys had been inoculated with one lot of 254 examples of *Culex* (*Culex*) *mouchetti* Evans from Bundinyama and two lots of *A. circumluteolus*, totalling 625 examples, from Kanyamwerima, an adjoining locality in the same gallery extension of the forest. The second monkey had received four lots of *A. cumminsi*, totalling 1,141 examples, from Bundinyama and Kanyamwerima, and one lot of 1,318 examples of the subgenus *Aëdimorphus* (26 of *Aëdes argenteopunctatus*, 74 of *A. mutilus*, 179 of the *A. abnormalis* group and 1,039 of *A. cumminsi*) from Bundinyama.

In addition, immunity had been found in wild Bwamba monkeys belonging to six species, of which two are strictly arboreal (Smithburn, Mahaffy & Haddow, 1944). It is very unlikely that these could have been infected by *A. abnormalis*, which is an inhabitant of the forest floor (as is *E. grahami*), and further, high rates of immunity in man were found at an early stage in the investigation in areas where *A. abnormalis* is not known to occur, for example, various Uganda localities, Tanganyika, South Africa, Egypt, India, Malaya and Borneo. It was concluded that this group represents only one among several vectors of the virus.

Subsequently it was shown by Drs. K. C. Smithburn and K. Goodner that while immune rates in man in Bwamba were moderately high (13 per cent.), they were extremely high in the Mbiru area near Entebbe (32 per cent. positive), and still later, in 1948, a woman living at Katabi, just outside Entebbe, who had suffered from an acute illness diagnosed as poliomyelitis, was found during convalescence to be immune to Semliki Forest virus. This finding is not conclusive, as she might have acquired her protective antibodies at an earlier time,

but it is very suggestive, as several other people in the same area were also shown to be immune and, more particularly, as a redtail monkey, *Cercopithecus ascanius schmidti*, from Katabi was also found to have a protective serum.

In 1943, a hitherto unknown agent known as Ntaya virus was isolated from a mixed lot of mosquitos taken in swamp forest in Bwamba County (Smithburn & Haddow, 1951). It is not possible to tell from which species the virus came. Among the mosquitos discussed here the only species represented in the infected lot was *A. albomarginatus*. It seems unlikely that this was the vector, as it is a rather scarce forest mosquito with a restricted distribution, whereas human surveys have shown that Ntaya virus occurs in various parts of Uganda, Tanganyika, Egypt, India, Malaya, Singapore and Borneo. The infection seems to be rather prevalent in Egypt, and this suggests that *Culex* spp. may be the natural vectors, as they have proved important in relation to other virus diseases in that area (Taylor & Hurlbut, 1953; Taylor & others, 1956). It is to be noted that the original infected lot of 1,318 mosquitos included 1,284 examples of *Culex* spp.

There were various isolations in 1944. One of the agents, Bunyamwera virus, which was isolated from mosquitos caught in the Semliki Forest in the vicinity of the Semliki River, will be discussed more fully below, as this isolation has a bearing on the importance of *A. circumluteolus* as a virus vector.

Later in the year, yellow fever virus was isolated from a mixed lot of *Aëdes* spp. taken in the Semliki Forest (Smithburn & Haddow, 1946). Various of the mosquitos discussed above were included in the infected lot, namely *A. simulans* (which at that time was referred to *A. haworthi*), *A. argenteopunctatus*, *A. mutilus*, *A. abnormalis* group, *A. lamborni*, *A. cumminsi*, *A. natronius*, *A. palpalis* and *A. taeniarostris*. On theoretical grounds, however, it was concluded that *A.* (*Stegomyia*) *africanus* (Theo.), which was also included in the infected lot, was much more likely than any of the above to be the local forest vector and this view was later substantiated (Haddow, Smithburn & others, 1948; Smithburn, Haddow & Lumsden, 1949). At the moment there is no reason to suppose that any member of the three subgenera here discussed is a natural vector of yellow fever though some species have been shown to be capable of transmitting or maintaining the virus in the laboratory. Thus Bauer (1928) found that *A.* (*A.*) *apicoannulatus* (at first assigned to *A. stokesi*) was an effective laboratory vector, and Philip (1930) showed that *A. irritans*, *A. nigricephalus* and *A. punctocostalis* can maintain the virus, though he did not obtain transmissions by bite. Similarly, Kitchen, Haddow & Smithburn (unpublished; quoted in Strode, 1951) found that *A. cumminsi* is capable of maintaining the virus.

In the same year, 1944, six isolations of Rift Valley fever virus were made from mosquitos taken in the Semliki Forest (Smithburn, Haddow & Gillett, 1948). First described as a disease of livestock (Daubney & Hudson, 1931), Rift Valley fever has also been reported frequently from laboratory workers who have been in contact with the virus (Kitchen, 1934; Smithburn, Mahaffy & others, 1949) and also in natural infections, which may have serious after-effects on vision (Mundel & Gear, 1951; Joubert, Ferguson & Gear, 1951; Gear, De Meillon & others, 1951; Gear & others, 1955). The visual defects have been studied particularly by Freed (1951). While the infection was first described from Kenya, the most serious recent outbreaks have been in the Union of South Africa. The number of mosquito species from which this dangerous virus has been isolated is now substantial, and four genera are known to be involved. In the Bwamba work, isolations were made from *Eretmapodites* spp., from *A.* (*S.*) *dendrophilus* Edw. (at that time assigned to *A.* (*S.*) *deboeri* ssp. *demeilloni* Edw.) and from the *A. tarsalis* group (two isolations). More recently there have been repeated isolations from mosquitos in the Union of South Africa, two of these being from *A. circumluteolus* (Kokernot, Heymann & others, 1957). In the Entebbe area

an atypical strain of Rift Valley fever virus has been isolated from the same species, which may well prove to be an important vector (Weinbren, Williams & Haddow, 1957). Thus two of the three subgenera here discussed are known to be involved in the epidemiology of this exceedingly important infection.

In 1947, Uganda S virus was isolated from a mixed lot of arboreal species of *Aëdes* taken in Bwamba (Dick & Haddow, 1952). The lot consisted of 47 examples of *A.* (*Finlaya*) *longipalpis* (Grünb.), 17 of *A.* (*F.*) *ingrami* Edw. and one of *A. natronius*. It is not possible to tell from which of these species the virus was derived. Humans immune to Uganda S virus have since been found in various other parts of Uganda, and in Tanganyika, Egypt, India, Malaya, Borneo and perhaps Brazil.

Recent work in the Union of South Africa, to be discussed below, has shown that *A. circumluteolus* is one of the most important of the known virus vectors of Africa. It is now necessary to return to the isolation of Bunyamwera virus (Smithburn, Haddow & Mahaffy, 1946), which, apart from the possible isolations of Semliki Forest virus referred to above, gave the first indication that this mosquito might be of interest. The isolation was made from a lot of 4,114 examples of *Aëdes* spp., of which 2,584 belonged to the subgenus *Banksinella* (*A. circumluteolus*, *A. palpalis*, and *A. taeniarostris*). The collection was made in dense forest and riverside thicket on the banks of the Semliki River. The virus may be regarded as an important one as it has been shown (in the case of one human volunteer) that severe encephalitis with residual mental symptoms may follow infection (Southam & Moore, 1951, 1954). It is also known, as a result of surveys in man, that it is active over a wide area, immunity having been found in various parts of Uganda, in Tanganyika, the Union of South Africa, Egypt, Borneo and Brazil. Further, it has recently been isolated from a naturally infected man in South Africa (K. C. Smithburn, personal communication).

Some interesting work was carried out in Bwamba after the isolation. Among 42 monkeys collected in widely distributed areas in the Semliki Forest, only one was immune, and this specimen was obtained within the catching area and actually during the catch from which the isolation was made. It appeared, therefore, that the focus of activity in the forest might be very localised. Surveys in man were next made in areas adjoining the Semliki Forest (which is closed to human habitation). Here the incidence of immunity was only about 4 per cent. In the Ruwenzori foothills, some miles away from the forest, the rate was about the same, 3 per cent. In the more open grassland and agricultural country which divides the foothills from the forest-edge zone the incidence was higher—about 10 per cent. On the other hand, on the open Semliki Plains north of the forest, the incidence was very high indeed—25 per cent. A point of great interest was that at the time when the catch was made at Bunyamwera there was a small illegal fishing settlement in the (officially closed) forest on the Congo side of the Semliki River almost opposite the catching area. These fishermen came from the Semliki Plains, and may well have introduced the virus with them—there was at that time a brisk illegal traffic in fish between the forest interior and the plains, cargoes being smuggled down by canoe. *A. circumluteolus* is abundant on the plains and also in the thickets along the Semliki River whereas most of the other species taken in the infected lot are more or less confined to forest. *A. circumluteolus* thus seemed by far the most likely suspect.

In Uganda this mosquito has been involved in only one other isolation (that of the variant of Rift Valley fever virus mentioned above) but, in the Union of South Africa, Smithburn and his colleagues have recently shown that it is a virus vector of major importance. During work in Tongaland there has been one isolation from it of Bunyamwera virus, one of Rift Valley fever virus, and one of the two mixed (Kokernot, Heymann & others, 1957). There have also been ten isolations of the newly discovered Pongola virus (Kokernot, Smithburn & others,

1957), one of a second new agent, Simbu virus (Weinbren & others, 1957), and one of a third, Wesselsbron virus (Smithburn, Kokernot & others, 1957). *A. circumluteolus* was also shown to be a good laboratory vector of the last-named virus (Muspratt & others, 1957). Since these isolations, seven others have been made (two of the agents are probably identical and probably new; three have been identified as Bunyamwera virus, one as Wesselsbron virus and one as Middelburg virus; K. C. Smithburn, private communication). The last named agent, like Wesselsbron, affects both sheep and man, and it is interesting to note that in the original isolations one strain was obtained from a pool of *Banksinella* spp. This pool consisted of *A. lineatopennis* and *A. albothorax*, or a very closely related form (Kokernot, De Meillon & others, 1957).

This last isolation is a most interesting one as it is the only one so far in which a member of the subgenus *Banksinella* other than *A. circumluteolus* has been definitely incriminated. Both *A. albothorax* and *A. lineatopennis* have a very wide African distribution, and *A. lineatopennis* spreads eastward to India and the Philippines. It is a notorious ' nuisance ' mosquito which may emerge in very large numbers after rain and invade towns, sometimes from relatively distant breeding foci. The writer witnessed one such invasion at Kisumu, Kenya, where the source of the mosquitos was found to be about four miles from the centre of the town. Another case has been described for Mombasa by Teesdale (1950). In this case *A. lineatopennis* and *A.* (*B.*) *albicosta* (Edw.) are given as the invading species, though according to Mrs. E. C. C. van Someren (private communication) the species involved were actually *A. albothorax* and *A. albicosta*. The habit of long travel in the form of invading swarms thus seems to be common in this subgenus. Its potential medical significance is obvious.

Summary.

The biting behaviour of East African species of *Aëdes* in the subgenera *Aëdimorphus*, *Banksinella* and *Dunnius*, as shown in numerous series of 24-hr. catches made predominantly in Uganda, is discussed. It is shown that with the single exception of *A.* (*A.*) *natronius* Edw., which is arboreal, all the species encountered have been most prevalent at ground level. They bite mostly by day, but *A. cumminsi* (Theo.) shows a marked peak of activity from just before to just after sunset, and *A. natronius* is crepuscular. When, however, samples were obtained in environments less favoured than the forest floor, and in which the mosquito concerned was less abundant, the biting cycle might be altered. Thus various species which were essentially diurnal at ground level in forest might be nocturnal in the canopy or in banana plantations.

In some cases there seemed to be a tendency towards a group pattern of behaviour. For example, in the *abnormalis* (Theo.) and *tarsalis* (Newst.) groups of Edwards it was found that at least three species showed very similar biting cycles. A fourth species, *A. nigricephalus* (Theo.), which occurs in Nigeria, is reported there to differ in its biting habits, and is also strikingly different in appearance and in the structure of the terminalia.

Members of all three subgenera have been involved in various isolations of virus, but it is not possible to prove that they, rather than other species of *Aëdes* included in the infected lots, were the vector mosquitos, except in the case of the *A. tarsalis* group, from which there have been two definite isolations of Rift Valley fever virus, and in that of *A. circumluteolus* (Theo.), which has been shown by recent work in South and East Africa to be of major importance, well over 20 isolations of virus having been made from this species. So far as is known at present, seven separate viruses and one distinct variant have been isolated from *A. circumluteolus*, and other members of the subgenus *Banksinella* also appear to be involved in transmission.

References.

Bauer, J. H. (1928). The transmission of yellow fever by mosquitoes other than *Aëdes aegypti*.—*Amer. J. trop. Med.* **8** pp. 261–282.

Causey, O. R. & Theiler, M. (1958). Virus antibody survey on sera of residents of the Amazon Valley in Brazil.—*Amer. J. trop. Med. Hyg.* **7** pp. 36–41.

Daubney, R. & Hudson, J. R. (1931). Enzootic hepatitis or Rift Valley fever. An undescribed virus disease of sheep, cattle and man from East Africa. —*J. Path. Bact.* **34** pp. 545–579.

De Meillon, B., Paterson, H. E. & Muspratt, J. (1957). Studies on arthropod-borne viruses of Tongaland. II. Notes on the more common mosquitoes.—*S. Afr. J. med. Sci.* **22** pp. 47–53.

Dick, G. W. A. & Haddow, A. J. (1952). Uganda S virus. A hitherto unrecorded virus isolated from mosquitoes in Uganda. I. Isolation and pathogenicity.—*Trans. R. Soc. trop. Med. Hyg.* **46** pp. 600–618.

Edwards, F. W. (1941). Mosquitoes of the Ethiopian Region. III. Culicine adults and pupae.—499 pp. London, Brit. Mus. (Nat. Hist.).

Freed, I. (1951). Rift Valley fever in man complicated by retinal changes and loss of vision.—*S. Afr. med. J.* **25** pp. 930–932.

Gear, J., De Meillon, B., Measroch, V., Harwin, R. & Davis, D. H. S. (1951). Rift Valley fever in South Africa. 2. The occurrence of human cases in the Orange Free State, the North-western Cape Province, the Western and Southern Transvaal. B. Field and laboratory investigations.—*S. Afr. med. J.* **25** pp. 908–912.

Gear, J. & others (1955). Rift Valley fever in South Africa. A study of the 1953 outbreak in the Orange Free State, with special reference to the vectors and possible reservoir hosts.—*S. Afr. med. J.* **29** pp. 514–518.

Haddow, A. J. (1942). The mosquito fauna and climate of native huts at Kisumu, Kenya.—*Bull. ent. Res.* **33** pp. 91–142.

Haddow, A. J. (1945*a*). The mosquitoes of Bwamba County, Uganda. II. Biting activity with special reference to the influence of microclimate.—*Bull. ent. Res.* **36** pp. 33–73.

Haddow, A. J. (1945*b*). The mosquitoes of Bwamba County, Uganda. III. The vertical distribution of mosquitoes in a banana plantation and the biting cycle of *Aëdes* (*Stegomyia*) *simpsoni*, Theo.—*Bull. ent. Res.* **36** pp. 297–304.

Haddow, A. J. (1952). Further observations on the biting-habits of Tabanidae in Uganda.—*Bull. ent. Res.* **42** pp. 659–674.

Haddow, A. J. (1954). Studies of the biting-habits of African mosquitos. An appraisal of methods employed, with special reference to the twenty-four-hour catch.—*Bull. ent. Res.* **45** pp. 199–242.

Haddow, A. J. (1956*a*). Observations on the biting-habits of African mosquitos in the genus *Eretmapodites* Theobald.—*Bull. ent. Res.* **46** pp. 761–772.

Haddow, A. J. (1956*b*). Rhythmic biting activity of certain East African mosquitoes.—*Nature, Lond.* **177** pp. 531–532.

Haddow, A. J. & Dick, G. W. A. (1948). Catches of biting Diptera in Uganda with anaesthetized monkeys as bait.—*Ann. trop. Med. Parasit.* **42** pp. 271–277.

HADDOW, A. J., GILLETT, J. D. & HIGHTON, R. B. (1947). The mosquitoes of Bwamba County, Uganda. V. The vertical distribution and biting-cycle of mosquitoes in rain-forest, with further observations on micro-climate.—*Bull. ent. Res.* **37** pp. 301–330.

HADDOW, A. J., GILLETT, J. D., MAHAFFY, A. F. & HIGHTON, R. B. (1950). Observations on the biting-habits of some Tabanidae in Uganda, with special reference to arboreal and nocturnal activity.—*Bull. ent. Res.* **41** pp. 209–221.

HADDOW, A. J., SMITHBURN, K. C., DICK, G. W. A., KITCHEN, S. F. & LUMSDEN, W. H. R. (1948). Implication of the mosquito *Aëdes* (*Stegomyia*) *africanus* Theobald in the forest cycle of yellow fever in Uganda.—*Ann. trop. Med. Parasit.* **42** pp. 218–223.

HALE, J. H., LIM, K. A. & LEE, L. H. (1956). Neutralizing antibodies against certain arthropod-borne viruses in the sera of Singapore and Borneo children.—*Ann. trop. Med. Parasit.* **50** pp. 268–274.

JOUBERT, J. D. S., FERGUSON, A. L. & GEAR, J. (1951). Rift Valley fever in South Africa. 2. The occurrence of human cases in the Orange Free State, the North-western Cape Province, the Western and Southern Transvaal. A. Epidemiological and clinical findings.—*S. Afr. med. J.* **25** pp. 890–891.

KITCHEN, S. F. (1934). Laboratory infections with the virus of Rift Valley fever. —*Amer. J. trop. Med.* **14** pp. 547–564.

KOKERNOT, R. H., DE MEILLON, B., PATERSON, H. E., HEYMANN, C. S. & SMITHBURN, K. C. (1957). Middelburg virus. A hitherto unknown agent isolated from *Aëdes* mosquitoes during an epizootic in sheep in the eastern Cape Province.—*S. Afr. J. med. Sci.* **22** pp. 145–153.

KOKERNOT, R. H., HEYMANN, C. S., MUSPRATT, J. & WOLSTENHOLME, B. (1957). Studies on arthropod-borne viruses of Tongaland. V. Isolation of Bunyamwera and Rift Valley fever viruses from mosquitoes.—*S. Afr. J. med. Sci.* **22** pp. 71–80.

KOKERNOT, R. H., SMITHBURN, K. C. & WEINBREN, M. P. (1956). Neutralizing antibodies to arthropod-borne viruses in human beings and animals in the Union of South Africa.—*J. Immunol.* **77** pp. 313–323.

KOKERNOT, R. H., SMITHBURN, K. C., WEINBREN, M. P. & DE MEILLON, B. (1957). Studies on arthropod-borne viruses of Tongaland. VI. Isolation of Pongola virus from *Aëdes* (*Banksinella*) *circumluteolus* Theo.—*S. Afr. J. med. Sci.* **22** pp. 81–92.

KUMM, H. W. & NOVIS, O. (1938). Mosquito studies on the Ilha de Marajó, Pará, Brazil.—*Amer. J. Hyg.* **27** pp. 498–515.

LUMSDEN, W. H. R. (1951). Probable insect vectors of yellow fever virus, from monkey to man, in Bwamba County, Uganda.—*Bull. ent. Res.* **42** pp. 317–330.

LUMSDEN, W. H. R. (1952). The crepuscular biting activity of insects in the forest canopy in Bwamba, Uganda. A study in relation to the sylvan epidemiology of yellow fever.—*Bull. ent. Res.* **42** pp. 721–760.

MACNAMARA, F. N. (1953). The susceptibility of chicks to Semliki Forest virus (Kumba strain).—*Ann. trop. Med. Parasit.* **47** pp. 9–12.

MATTINGLY, P. F. (1949). Studies on West African forest mosquitos. Part II. The less commonly occurring species.—*Bull. ent. Res.* **40** pp. 387–402.

MUNDEL, B. & GEAR, J. (1951). Rift Valley fever. I. The occurrence of human cases in Johannesburg.—*S. Afr. med. J.* **25** pp. 797–800.

Muspratt, J., Smithburn, K. C., Paterson, H. E. & Kokernot, R. H. (1957). Studies on arthropod-borne viruses of Tongaland. X. The laboratory transmission of Wesselsbron virus by the bite of *Aëdes* (*Banksinella*) *circumluteolus* Theo.—*S. Afr. J. med. Sci.* **22** pp. 121–126.

Philip, C. B. (1930). The experimental transmission of yellow fever by mosquitoes.—*Science* **71** pp. 614–615.

Smithburn, K. C. (1952). Neutralizing antibodies against certain recently isolated viruses in the sera of human beings residing in East Africa.—*J. Immunol.* **69** pp. 223–234.

Smithburn, K. C. (1954). Neutralizing antibodies against arthropod-borne viruses in the sera of long-time residents of Malaya and Borneo.—*Amer. J. Hyg.* **59** pp. 157–163.

Smithburn, K. C. & Haddow, A. J. (1944). Semliki Forest virus. I. Isolation and pathogenic properties.—*J. Immunol.* **49** pp. 141–157.

Smithburn, K. C. & Haddow, A. J. (1946). Isolation of yellow fever virus from African mosquitoes.—*Amer. J. trop. Med.* **26** pp. 261–271.

Smithburn, K. C. & Haddow, A. J. (1951). Ntaya virus. A hitherto unknown agent isolated from mosquitoes collected in Uganda.—*Proc. Soc. exp. Biol.* **77** pp. 130–133.

Smithburn, K. C., Haddow, A. J. & Gillett, J. D. (1948). Rift Valley fever. Isolation of the virus from wild mosquitoes.—*Brit. J. exp. Path.* **29** pp. 107–121.

Smithburn, K. C., Haddow, A. J. & Lumsden, W. H. R. (1949). An outbreak of sylvan yellow fever in Uganda with *Aëdes* (*Stegomyia*) *africanus* Theobald as principal vector and insect host of the virus.—*Ann. trop. Med. Parasit.* **43** pp. 74–89.

Smithburn, K. C., Haddow, A. J. & Mahaffy, A. F. (1946). A neurotropic virus isolated from *Aëdes* mosquitoes caught in the Semliki Forest.—*Amer. J. trop. Med.* **26** pp. 189–208.

Smithburn, K. C., Kerr, J. A. & Gatne, P. B. (1954). Neutralizing antibodies against certain viruses in the sera of residents of India.—*J. Immunol.* **72** pp. 248–257.

Smithburn, K. C., Kokernot, R. H., Weinbren, M. P. & De Meillon, B. (1957). Studies on arthropod-borne viruses of Tongaland. IX. Isolation of Wesselsbron virus from a naturally infected human being and from *Aëdes* (*Banksinella*) *circumluteolus* Theo.—*S. Afr. J. med. Sci.* **22** pp. 113–120.

Smithburn, K. C., Mahaffy, A. F. & Haddow, A. J. (1944). Semliki Forest virus. II. Immunological studies with specific antiviral sera and sera from humans and wild animals.—*J. Immunol.* **49** pp. 159–173.

Smithburn, K. C., Mahaffy, A. F., Haddow, A. J., Kitchen, S. F. & Smith, J. F. (1949). Rift Valley fever. Accidental infections among laboratory workers.—*J. Immunol.* **62** pp. 213–227.

Smithburn, K. C., Taylor, R. M., Rizk, F. & Kader, A. (1954). Immunity to certain arthropod-borne viruses among indigenous residents of Egypt.—*Amer. J. trop. Med. Hyg.* **3** pp. 9–18.

Southam, C. M. & Moore, A. E. (1951). West Nile, Ilheus, and Bunyamwera virus infections in man.—*Amer. J. trop. Med.* **31** pp. 724–741.

Southam, C. M. & Moore, A. E. (1954). Anti-virus antibody studies following induced infection of man with West Nile, Ilhéus, and other viruses.—*J. Immunol.* **72** pp. 446–462.

Strode, G. K. *Ed.* (1951). Yellow fever.—710 pp. New York, McGraw-Hill.

Taylor, R. M. & Hurlbut, H. S. (1953). The isolation of Coxsackie-like viruses from mosquitoes.—*J. Egypt. med. Ass.* **36** pp. 489–494.

Taylor, R. M., Work, T. H., Hurlbut, H. S. & Rizk, F. (1956). A study of the ecology of West Nile virus in Egypt.—*Amer. J. trop. Med. Hyg.* **5** pp. 579–620.

Teesdale, C. (1950). An apparent invasion of *Aëdes* (*Banksinella*) *lineatopennis* and *Aëdes* (*B.*) *albicosta* into Mombasa Island.—*Proc. R. ent. Soc. Lond.* (A) **25** pp. 99–102.

Weinbren, M. P., Heymann, C. S., Kokernot, R. H. & Paterson, H. E. (1957). Studies on arthropod-borne viruses of Tongaland. VII. Simbu virus, a hitherto unknown agent isolated from *Aëdes* (*Banksinella*) *circumluteolus* Theo.—*S. Afr. J. med. Sci.* **22** pp. 93–102.

Weinbren, M. P., Williams, M. C. & Haddow, A. J. (1957). A variant of Rift Valley fever virus.—*S. Afr. med. J.* **31** pp. 951–957.

Williams, C. B. (1937). The use of logarithms in the interpretation of certain entomological problems.—*Ann. appl. Biol.* **24** pp. 404–414.

Appendix.

The use of the geometric mean has much to recommend it in treating the numerical results of catches such as are discussed in this paper. Unfortunately, it cannot be used in the case of a series in which zero values occur. A solution to this difficulty was found by Williams (1937) and the method he devised is beginning to be used widely. So far, entomologists who have employed this particular measure of the central tendency have referred to it loosely as " the geometric mean " or " Williams' modification of the geometric mean ", and the symbol M_G has been used to denote it, as have other symbols, all containing the letter G. In following this usage in an earlier paper, it was pointed out that the figure obtained is not strictly the geometric mean and should be given a name of its own (Haddow, 1954). The author proposes that in future the use of the word " geometric " in this connection should be discontinued and that the measure should be termed " Williams' mean ", denoted by the symbol M_w, defined by

$$\log (M_w + 1) = \frac{\Sigma \log (n + 1)}{N}$$

where n_1, n_2 . . . represent the actual values of a series of N observations. M_w is thus obtained by subtracting 1 from the antilogarithm of the quantity found by first adding 1 to each of the original observations, then summing the logarithms of the numbers so obtained, and finally dividing by the total number of observations.

© Commonwealth Agricultural Bureaux, 1959.

INSECTICIDE STUDIES ON EAST AFRICAN AGRICULTURAL PESTS.

III.—SEED DRESSINGS FOR THE CONTROL OF THE BEAN FLY, *MELANAGROMYZA PHASEOLI* (COQ.), IN TANGANYIKA.

By P. T. Walker

Colonial Pesticides Research Unit, Porton Down, Salisbury, England.

The bean fly, *Melanagromyza phascoli* (Coq.) is a cosmopolitan pest of beans and other leguminous crops. It occurs widely throughout the warmer parts of the world, having been recorded from East Africa, Rhodesia, Australia, Ceylon, Mauritius, Java and Egypt.

In Tanganyika, a serious outbreak occurred in 1955, and some loss is expected during most years. The amount of damage due to the pest depends on the intensity of the attack and on the weather. During an adverse year, plants are unable to withstand a severe attack and loss results, but if conditions are favourable up to 50 per cent. of the plants can be attacked without great loss. The latter was the case in most areas of the Northern Province in 1956. In Arusha, the maximum infestations found in tall plants seldom reached five to ten larvae per plant. On the other hand, during severe attacks in Egypt, for instance, 25 larvae and puparia have been recorded in plants only eight in. high.

Life-history.

The white elongated eggs are about 1 mm. in length and are laid singly on the lower parts of the stems above the surface of the ground. Newly emerged larvae tunnel in the stems, macerating and destroying the tissue and eventually causing the plant to wither and fall. In addition, van Someren (1956) has recorded that the fly will also lay eggs at the base of the petioles. Lesions produced there by the larvae were considered to be the cause of yellowing and stunting of the leaves and the typical reaction of the plant to bean-fly attack. The grower, in the case recorded, confused the attack with the effects of drought. Van Someren also remarks that if plentiful rain falls on attacked plants, the growth of adventitious roots above the stem lesions will often allow the plants to survive. Often primary lesions caused by the bean fly are the means by which termites enter and kill the plant.

Larvae pupate near the surface of the stem, either under the epidermis or in open cracks. The puparia are dark brown to black, about 3 mm. long, and are usually seen plentifully by April under normal conditions. The pupal period is eight to ten days, and the adults are small black flies, about 1·5 to 2 mm. long.

The actual duration of the various stages has not been investigated, but puparia can be found three to four weeks after plants germinate. In Mauritius, a period of 20 days has been given for the time of development from egg to adult, and young larvae have been found active in the stems six to seven days after the appearance of the cotyledons (Moutia, 1945).

Previous Work on Control Measures.

Nicotine and oil sprays had been used before DDT was tested in Mauritius (Moutia, *op. cit.*) and in Australia (Hely, 1948). DDT as a 2 per cent. dust seems

to have been less effective than as an emulsion spray at strengths of 0·05 to 0·5 per cent. A five-fold increase in yield has been recorded in Mauritius by Moutia (1946). Final recommendations were a 0·05 per cent. DDT emulsion spray applied once a week from the third or fifth day that the plants were above the ground until just before blossoming.

The danger of an increase of Tetranychid mites is mentioned, and it is recommended that they should be controlled by an application of lime-sulphur.

Later work with dusts and sprays has shown that frequent applications of DDT, BHC and toxaphene are effective (van der Laan, 1949), as well as DDD. Diazinon, dieldrin and parathion (Braithwaite, 1957).

There is evidence that varieties differ in their susceptibility to bean-fly attack. Different species of bean certainly show different degrees of attack.

It has been found in recent years that dressing seeds with insecticides will prevent or reduce the attack on seeds and stems by pests. Some of the evidence is reviewed later, in the Discussion. The method, if successful, offers a simple and cheap means of controlling bean fly.

Reports on the effectiveness of insecticides for this purpose have been conflicting, however. The degree of infestation by bean fly varies greatly from year to year and from place to place, and, as already pointed out, the losses from this pest are likewise variable. A series of trials was therefore put down in 1956 and 1957 in order to assess the effect of insecticides under different growing conditions.

The 1956 Trials.

Two trials were laid out in the Loljoro Valley, near Arusha, Tanganyika; one being devoted to dry dressings and the other to wet dressings. White haricot beans, *Phaseolus vulgaris*, were sown at a rate of about 20 lb./acre with a Planet hand drill in plots 10 yd. × 3 rows (1½ ft. apart), or approx. 1/320 acre, in size, arranged in randomised blocks, seven treatments being replicated four times. The beans were sown on 10th April and germinated 6–8 days later, but a drought soon after sowing considerably affected germination and growth. For this reason final yields were not taken.

Observations were made on the rate of infestation by bean fly. The first occasion on which eggs were found was the 1st May and the percentages of plants attacked, based on counts of ten plants per replicate made on 11th and 18th May, are shown in figs. 1 and 2.

Wet dressings (Trial A).

A simple method of depositing a thin film of insecticide on the seed coat is to moisten seeds with the emulsifiable concentrate (EC) of the insecticide. As these

TABLE I.

Rates of application of wet dressings, 1956.

Insecticide	Strength of EC* (%)	Rate of application per lb. seed	
		EC (ml.)	Insecticide (g.)
Aldrin ..	24	3·8	0·91
Endrin ..	19·5	4·6	0·90
Dieldrin ..	18	5·04	0·91
γ BHC ..	20	4·6	0·92
DDT ..	25	3·6	0·90
Malathion ..	50	1·82	0·91

* Emulsifiable concentrate.

formulations incorporate a high proportion of hydrocarbon solvent, which is usually phytotoxic, it has been found that seeds must remain in contact with the concentrate for the shortest possible time in order to avoid damage. In practice, 1 lb. seed was mixed quickly with the required volume of concentrate and then put on absorbent paper to dry. If long contact was allowed, blistering and wrinkling of the testa occurred; this could interfere with drilling. The treatments used, in addition to the control (no dressing), were as shown in Table I.

These rates are approximately equal to an application of 0·2 per cent. of insecticide w/w of seed. Not all the insecticide applied to the seeds reached the soil, but this aspect was not investigated in the first trials.

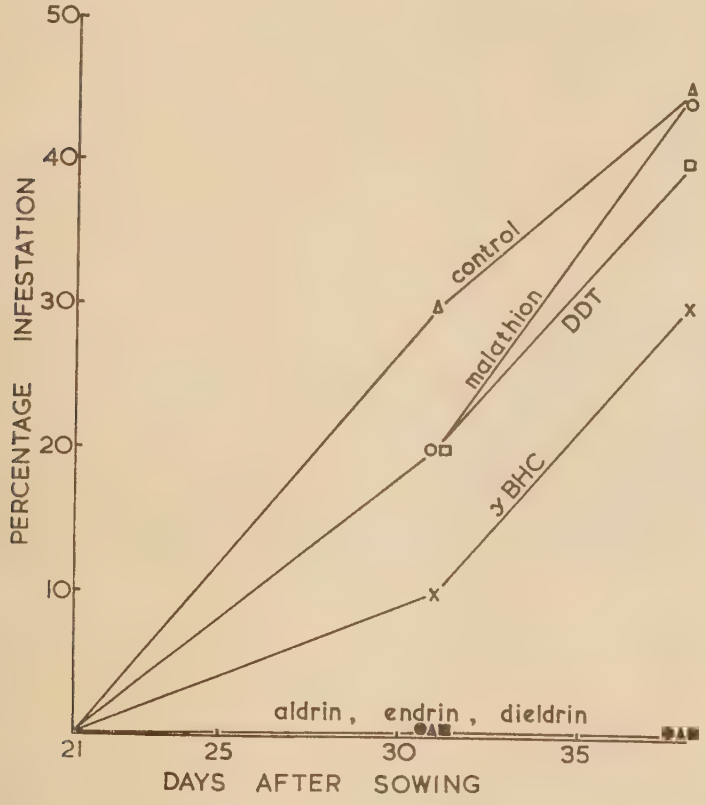


Fig. 1.—The course of infestation of bean plants by *M. phaseoli* after application of various wet insecticidal dressings to the seed.

There was some phytotoxic effect with all the treatments, as is shown by the following counts of plant numbers taken 30 days after sowing (Table II). This effect is partly due to the poor growing conditions, but it will be seen that a similar reduction in germination occurs in a laboratory germination test.

The course of bean-fly attack on the treated material is shown in fig. 1. It will be seen that aldrin, endrin and dieldrin gave complete protection against attack for at least 30 days after germination while the plants from untreated seeds developed a 45 per cent. infestation. Treatment with γ BHC resulted in less attack than the controls but even so infestation rose to 30 per cent. Malathion and DDT had little effect.

TABLE II.

Phytotoxic effects of wet dressings, 1956.

Treatment	Sample plant stand as % of the control (mean of 4 counts)	% Germination in laboratory
Aldrin	76	80
Endrin	70	87
Dieldrin	57	62
γ BHC	56	45
DDT	54	64
Malathion	94	66
Control	100	88

Dry dressing (*Trial B*).

The use of both properly formulated seed dressings and wettable powders for application in the dry state to seeds is well established. In this trial somewhat heavy dressings were used, sometimes in excess of the amount that could be carried by the beans. It is possible, therefore, that not all the dose stated was carried into the ground. This factor is discussed later in the 1957 trials.

The treatments used, in addition to the control (no dressing), were as shown in Table III. This also shows the extent to which germination was depressed, estimated from counts of mean numbers of plants, expressed as a percentage of those in the control; it is considered that drought considerably accentuated this effect.

TABLE III.

Rates of application and phytotoxic effects of dry dressings, 1956.

Insecticide	Strength and type of formulation	Rate of application (% w/w seed)	Germination (% of control)
Aldrin	40% WP*	0·41	81·3
Dieldrin ..	25% WP	0·40	65·0
γ BHC	20% Dry dressing	0·25	80·8
Parathion ..	15% WP	0·24	67·5
Dipterex ..	50% WP	0·42	31·5
Diazinon ..	40% WP	0·41	33·0

* Wettable powder. The rate given above for aldrin is equivalent to 1 lb. of a wettable powder, containing 40 per cent. aldrin, per 100 lb. of bean seed.

Percentage infestations are shown in fig. 2. Aldrin was as effective as in trial A and γ BHC also completely prevented attack. Dieldrin, parathion and diazinon were less effective, and Dipterex was hardly superior to the control. Infestation in the control rose to 45 per cent.

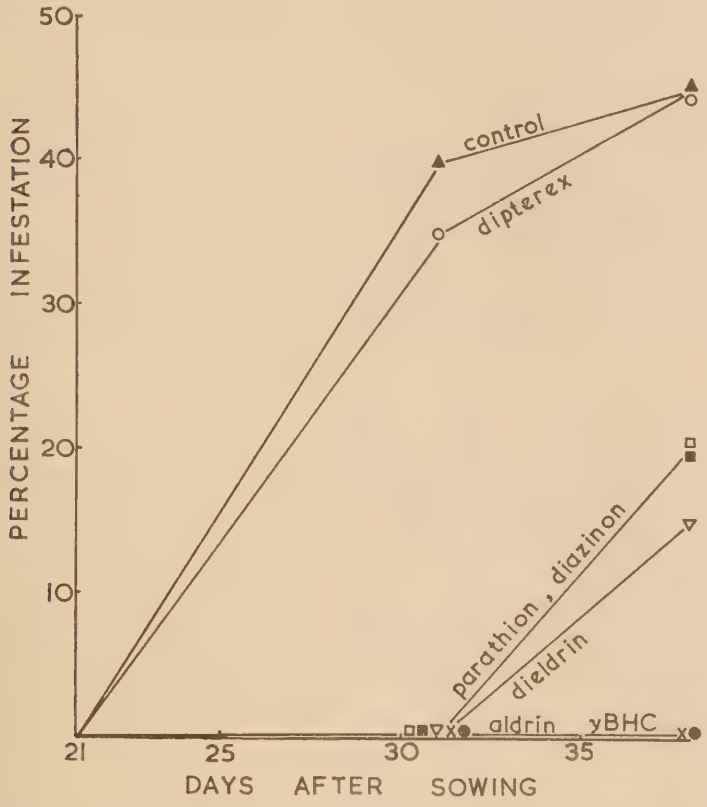


Fig. 2.—The course of infestation of bean plants by *M. phaseoli* after application of various dry insecticidal dressings to the seed.

The 1957 Trials.

Insecticides and treatments.

The insecticides and the formulations in which they were used are given below. The concentration of active ingredient given here was determined chemically and in many cases differed from that stated by the commercial suppliers.

1. *Aldrin wettable powder* (32% aldrin w/w) applied as a dry dressing at 3 g. per 1 lb. seed; equivalent to 211 mg. aldrin per 100 g. seed.
2. *Aldrin emulsifiable concentrate* (25·65% aldrin w/v) applied as a wet dressing at 3·8 ml., made up to 5 ml. with water, to 1 lb. seed; equivalent to 215 mg. aldrin per 100 g. seed.
3. *Aldrin wettable powder* (32% aldrin w/w) applied as a wet dressing at 3 g. per 1 lb. seed, with the addition of 5 ml. water to the dressed seed.

4. *Endrin emulsifiable concentrate* (21% endrin w/v) applied as a wet dressing at 4·6 ml., made up to 5 ml. with water, to 1 lb. seed; equivalent to 213 mg. endrin per 100 g. seed.
5. *γ BHC dry dressing* (a proprietary mercurial/γ BHC dressing containing 45·9% γ BHC w/w) applied as a dry dressing at 3 g. per 1 lb. seed; equivalent to 303 mg. γ BHC per 100 g. seed.
6. *γ BHC emulsifiable concentrate* (19·5% γ BHC w/v) applied as a wet dressing at 4·6 ml., made up to 5 ml. with water, to 1 lb. seed; equivalent to 197 mg. γ BHC per 100 g. seed.
7. *Dieldrin dry dressing* (a proprietary mercurial/dieldrin dressing containing 17·2% dieldrin w/w) applied as a dry dressing at 2 g. per 1 lb. seed; equivalent to 76 mg. dieldrin per 100 g. seed.
8. *Dieldrin emulsifiable concentrate* (17·8% dieldrin w/v) applied as a wet dressing, undiluted, at 5·04 ml. per 1 lb. seed; equivalent to 198 mg. dieldrin per 100 g. seed.
9. *V.P. 2823* (an organophosphorus systemic dry dressing of unknown constitution and concentration) applied at 2 g. per 1 lb. seed. This was considered to be the highest rate at which the dressing, which was light and flocculent, would adhere to the seed without leaving an excessive residue. The recommended rate of dressing was higher.
10. *Control*, no dressing.

Method of treatment.

In the absence of accurate knowledge of the amounts of dressing that can be taken up by bean seeds, those applied were based partly on commercial recommendations and partly on the 1956 trials already described. Usually a lower rate was used than was found to be effective in 1956.

Dry dressings were applied by sprinkling the required amount over the seed beans in paper bags and shaking for a constant time. Not all of it was taken up by the seeds, although there was no great surplus. Some surplus was also observed to remain in bags and in the hopper of the drill after drilling, indicating that the amount of dressing actually available in the ground is always less than that applied to the seed. Chemical data in support of this are given below.

TABLE IV.

Amount of insecticide retained by seeds after dressing.

Nature	No.	Rate of application (mg./100g. seed)	Amount retained (mg./100g. seed)		% retained	
			Sample 1	Sample 2	Sample 1	Sample 2
Dry	1	211	45·7	39·5	21·7	18·7
	5	303	76·1	72·9	25·1	24·1
	7	76	21·8	24·5	28·7	32·2
Wet	2	215	111·6	96·0	51·9	44·7
	4	213	101·4	119·9	47·6	56·3
	6	197	130·4	97·0	66·2	49·2
	8	198	107·2	91·6	54·1	46·3
Wet/Dry	3	211	99·2	170·1	47·0	80·6*

* No explanation can be given for this anomalous result.
Seeds from treatment 9 were not analysed.

Wet dressings were similarly agitated with the seed in a closed container for a constant time for each treatment, this being the minimum time necessary to give uniform wetting, and the wet seeds were then immediately spread out on hessian to dry, a volume of 5 ml. of liquid was found to wet 1 lb. of seed uniformly without any liquid residue.

In treatment no. 3, seeds were dressed dry with a wettable powder (aldrin), then wetted with the same amount of liquid, in this case water, as the wet dressings, and then dried. This resembles the slurry method of seed treatment.

Chemical analysis of uptake.

The residues on dressed seed that remained on two of the trials in the hopper of the seed drill after drilling the plots were analysed to determine the amount of active ingredient still retained by the seed; unfortunately no record was kept as to which of the trials were concerned, and the results are therefore referred to as samples 1 and 2 (Table IV). These figures show the actual amounts of insecticide carried into the soil on the seed. An unknown quantity of insecticide residue also fell from the hopper with the seed.

It will be seen that far greater amounts of insecticide were recovered when it was applied as a wet dressing, showing that seeds should either be treated with a liquid formulation or be moistened after application of a dry dressing.

Germination.

Treated seeds were tested under standard conditions for any adverse effects on germination. Apart from a general reduction of about 5 per cent. on the untreated germination rate of 90 per cent., no conclusive effect was observed. Seeds treated with γ BHC (no. 6), however, germinated about five days later than the rest, and this delay in germination was also obvious in the field.

Sowing details.

Trials were put down using dwarf haricot-type beans, *Phaseolus vulgaris*, on four sites in the Arusha district of the Northern Province of Tanganyika. Trial A was planted on a red clay soil in the usually drier area of the Loljoro Valley, trial B on black clay soil on the wetter slopes of Mount Meru at Usa River. Trials C and D were in the Olmotonyi area of Arusha and sown on porous volcanic soils, with average rainfall expectation.

A Planet seed drill was used to drill the plots by hand, the hopper being cleaned out between treatments. Seeds were sown to a depth of 1–2 in. and at a rate of about 26 lb. seed per acre.

Plots were sown during the rains, trial A on 8th April, B on 10th April, C

TABLE V.

Treatments ranked according to the weight of seed sown (decreasing).

Trial	Sowing conditions	Treatments									
A	Dry	*3*	*8*	1	*2*	*4*	*6*	9	*5*	*7*	10
B	Damp	10	5	7	9	1	*8*	*2*	*4*	*6*	*3*
C	„	10	7	1	5	*6*	*8*	9	*2*	*3*	*4*
D	„	1	5	7	9	10	*3*	*8*	*2*	*4*	*6*

Wet treatments are italicised.

TABLE VI.

Mean damage ratings (transformed data).

Insecticide and treatment no.	Trial A			Trial B			Mean of both trials		
	Dry	Wet	Mean	Dry	Wet	Mean	Dry	Wet	Mean
Aldrin, dry (1) & wet (2)	25·0	20·7	22·8	32·0	22·2	27·1	28·5	21·4	25·0
γ BHC, dry (5) & wet (6) ..	31·5	7·8	19·6	39·8	37·6	38·7	35·7	22·7	29·2
Dieldrin, dry (7) & wet (8) ..	12·4	12·4	12·4	17·0	27·3	22·1	14·7	19·9	17·3
S.E.	±4·46		±3·16	±4·46		±3·16	±3·16		±2·24
Mean	23·0	13·6	—	29·6	29·0	—	26·3	21·3	—
S.E.	±2·58			±2·58			±1·83		
Endrin, wet (4)	3·2			12·2			7·7		
Aldrin, wet/dry (3)	12·2			15·4			13·8		
V.P. 2823, dry (9)	56·0			55·2			55·6		
Control (10)	58·8			46·5			52·6		
S.E.	± 4·46			± 4·46			± 3·16		
Mean of all except 6, 9 & 10 ..	14·3			21·0					
S.E.	± 1·8			± 1·8					

on 3rd May and D on 4th May. Heavy rain made it impossible to reach trial A until 13th May, when the first pupae were found. Samples from this trial were taken on 25th May for estimation of damage.

Trial A was harvested on 11th July, C on 19th August, and D at the end of August. Trial B could not be harvested, but a record of damage was taken on 31st May.

The design and plot size in each trial was the same as in the 1956 trials (4 replications; plots approx. 1/320 acre).

The amount of seed sown bore an interesting relation to the type of dressing and possibly to the conditions of the trial. If treatments are ranked in decreasing order of the weight of seed sown (Table V), it is apparent that wet dressings (italicised) tend to be drilled at a lower rate than dry dressings, except in trial A, in which the conditions of soil and air at the time of sowing were drier than in other trials. It is possible, therefore, that in moist conditions wet-dressed seed clogs or sticks in the hopper of the drill, thus giving a lower seeding rate. A correction was applied to the yields for the weight of seed drilled per treatment.

Infestation and assessment of damage.

Samples of ten plants per replicate (40 per treatment) were pulled up and taken to the laboratory. The number infested by bean fly, the number of larvae and puparia found on examination and dissection, and the degree of damage, were recorded. The degree of damage was given a rating, based on the extent of splitting and rotting of the stem and root: no damage, 0; little damage, 1; severe damage, 2.

The three methods of assessment were in very close agreement, so there was no doubt that the damage recorded was due to bean fly, but as the damage ratings gave the most sensitive estimate of the effects of the different treatments, these alone were analysed. The percentage of plants attacked ranged from 2·5 (treatment 4, endrin) to 92·5 (control). The number of larvae and puparia found per 40 plants ranged from *nil* (treatment 4, endrin) to 43 (treatment 9, organophosphorus insecticide). In some cases, damage was present but no larvae or puparia (full or empty) could be found, the empty puparia probably having fallen or been blown away.

The total sample damage ratings were expressed as fractions of the maximum possible sample score, and transformed to angles. An analysis of variance showed a significant treatment-trials interaction at the 1 per cent. level of probability, suggesting that the results from individual trials would be of greater interest than the over-all means. The treatment means and their standard errors are given in Table VI for the two trials from which damage measurements were taken. Those treatments consisting of either wet or dry dressings of the same insecticide are grouped factorially in order to allow comparison of the two methods of dressing. In this analysis, a difference between means equal to about three times the standard error is significant at the 5 per cent., and of about four times at the 1 per cent., level of probability.

All treatments except V.P. 2823 had some effect and endrin was outstanding. Aldrin was much more effective when applied as a dry dressing that was then wetted than as either a dry or a wet dressing. The marked effectiveness of γ BHC as a wet dressing in trial A is thought to be due to the particular soil and weather conditions in that trial.

Although damage to the control was greater in trial A than in B, the reverse is the case in all the effective treatments. This implies that on trial A the attack was greater, but the insecticide treatments were more effective. Such a conclusion agrees with other information which suggests that insecticide treatments are more valuable under marginal growing conditions, when the survival

TABLE VII.

Mean yields of pods (oz. per treatment) for three trials.

Insecticide and treatment no.	Trial A			Trial C			Trial D			Mean of 3 trials		
	Dry	Wet	Mean	Dry	Wet	Mean	Dry	Wet	Mean	Dry	Wet	Mean
Aldrin, dry (1) & wet (2)	4·3	5·3	4·8	18·9	19·1	19·0	8·5	15·0	11·7	10·6	13·1	11·85
γ BHC, dry (5) & wet (6)	3·6	4·3	3·9	14·7	16·9	10·8	7·8	13·5	10·6	8·7	11·6	10·13
Dieldrin, dry (7) & wet (8)	4·4	4·8	4·6	16·7	11·5	14·1	10·1	10·1	10·1	10·4	8·8	9·6
S.E.	±1·09		±0·77	±1·09		±0·77	±1·09		±0·77	±0·63		±0·45
Mean	4·1	4·8		16·8	15·8		8·8	12·9		9·9	11·2	
S.E.	±0·63			±0·63			±0·63			±0·36		
Endrin, wet (4)		6·3			20·8			13·2			13·5	
Aldrin, wet/dry (3) ..		2·6			18·7			10·1			10·5	
V.P. 2823, dry (9) ..		1·9			16·9			9·3			9·4	
Control (10)		3·7			13·7			8·4			8·6	
S.E.		± 1·09			± 1·09			± 1·09			± 0·63	

of the crop is in doubt. A well-grown healthy crop often obtains little assistance from insecticide seed dressings.

Yields.

It was possible to obtain yields from only three of the four trials. When completely dry, the plants were pulled up by hand and the pods removed and weighed. Yields were corrected for the small variation in the amount of seed sown, and expressed as ounces of pods per treatment, each treatment covering approximately an eightieth of an acre. As there was a significant treatment/trials interaction, the yields from each trial are given in Table VII, with their respective standard errors.

Endrin (treatment 4) usually gave the highest yield, being most effective, relative to the control, under the poorer conditions of trial A, but its over-all mean did not differ significantly from that of aldrin applied as a wet dressing (treatment 2); both were superior to γ BHC as a wet dressing (treatment 6).

The method of wet dressing, as a whole, was more effective than dry dressing with the same insecticides.

Relation between infestation and yield.

Unfortunately an over-all regression of yield on infestation or damage cannot be calculated for all the trials, as comparable figures from each trial are not available. A valid regression can, however, be calculated for Trial A. The correlation coefficient r is $-0{\cdot}391$ (38 degrees of freedom, P approximately $= 0{\cdot}01$).

The equation for the regression of yield (Y), in units of dry pods, on bean-fly damage (x), expressed as a percentage of the maximum transformed to angles, is:

$$Y = 5{\cdot}0 - bx$$
$$\text{where } b = 0{\cdot}036 \pm 0{\cdot}0139 \text{ (for 38 degrees of freedom).}$$

There is no doubt that this correlation is a measure of the relation between depression of yield and attack by bean fly, and enables one to conclude, for example, that if the degree of damage by bean fly is reduced from 50 per cent. of the maximum possible damage to 10 per cent., an increase in yield of dry pods of just under a third might be expected, *i.e.*, from 3·38 to 4·34 units. It should be stressed however, that this conclusion is strictly valid only under the conditions of Trial A and within the range of results obtained from it. Because of the arbitrary method of rating the damage, and the poor growing conditions of Trial A, results are needed from other trials, under different conditions and assessed by a standard method, in order to obtain a full picture of the effect of seed dressings on bean-fly attack.

Discussion.

These results confirm those of van Someren (1956) regarding the efficacy of the chlorinated hydrocarbon insecticides. He obtained complete prevention of bean-fly attack in northern Tanganyika by dieldrin, as a dry dressing, at a probable rate of 0·04 per cent. active ingredient w/w seed, and also by chlordane at 0·55 per cent. Aldrin as a dry dressing at 0·44 per cent. was almost completely effective. Two organophosphorus insecticides, Hanane and Pestox 3, of which the active ingredients are dimefox and schradan, respectively, applied at 0·55 and 0·33 per cent. of active ingredient, respectively, were less effective.

Similar trials to control *Hylemyia cilicrura* (Rond.), by application of insecticidal dressings to seed beans have been reported by Ditman, Cox & Kantzes (1956). They also found considerable variation in the effect of different treatments under

different conditions, and mention the weather, temperature and soil moisture, seed variety and vitality, and the flora and fauna of the soil. They found that little benefit was to be obtained from seed dressings under either extremely favourable or unfavourable conditions, but that excellent responses resulted between these extremes. Starks & Lilly (1955) also report work on the seed dressing of beans.

The results of the present trials suggest that the effectiveness of seed dressings may be influenced by the amount of insecticide actually retained on the seed. Certainly more insecticide was carried on the seeds after wet dressing than after dry, and it can be seen that some of the treatments had an effect even at comparatively low retention rates. The most noticeable of these was the dry dressing of dieldrin, which gave quite good results although effectively applied at about one-fifth of the rate of active ingredient of most wet dressings. Aldrin dry treatment was likewise promising at a low effective rate.

Further trials are needed to show whether endrin is consistently superior, in terms of economic efficiency, to other chlorinated hydrocarbons, having regard to the variation in environmental conditions that seem to affect the results so markedly. It is suggested that more consistent results might be obtained from more accurately sown plots in prepared seed-beds, rather than from the drilled plots on a semi-field scale that were used here.

Summary.

The bean fly, *Melanagromyza phaseoli* (Coq.), the larvae of which tunnel in the stems of *Phaseolus vulgaris*, is a pest of this crop in Tanganyika. Field trials there in 1956 on haricot-type beans showed that dressing the seed with chlorinated-hydrocarbon insecticides could prevent attack for at least 30 days after germination; organophosphorus insecticides were less effective. In four further field trials (A–D), in 1957, the insecticides and types of formulation used were aldrin (wettable powder and emusifiable concentrate (EC)), endrin (EC), γ BHC (dry dressing and EC), dieldrin (dry dressing and EC) and a proprietary organophosphorus systemic (dry dressing). Wet dressings were applied by treating the seeds with the liquid and drying immediately, and in one treatment aldrin as a wettable powder was applied dry and the seeds then damped and dried at once.

Damage was assessed on an arbitrary scale on trials A and B, and yields measured on trials A, C and D. Results varied between insecticides and under different growing conditions, but wet dressing with endrin at 213 mg. per 100 g. seed, of which about 50 per cent. was retained on the seeds, resulted in the lowest damage, amounting to 7·7 compared with 52·6 for the control (no dressing), and the highest yield, amounting to 13·5 units compared with 8·6 for the control. All treatments, except that with the organophosphorus dust, reduced the damage significantly below that in the control. Wet dressings were usually more effective than dry dressings with the same insecticide, as regards both yield and reduction in damage. This may be associated with the better retention of wet dressings, which was shown by the results of chemical analysis of the residues on the seeds left in the drill hopper after sowing.

Acknowledgements.

I am indebted to Mr. Cameron of Loljoro and Mr. Mahon of Arusha for permission to carry out trials on their land and for facilities and help, to Dr. K. C. Sleep for chemical analyses, to Mr. K. S. MacKinlay for taking some yields during my absence, to Messrs. Westmacott and Vernon of Rothamsted for help with the statistical analysis, and to Mr. M. Kamya, Mr. V. Mdoe and others for assistance.

I am also indebted to Messrs. Shell Chemicals (East Africa) Ltd.; African Explosives and Chemical Industries (East Africa) Ltd.; Plant Protection Ltd.;

Fison's Pest Control (East Africa) Ltd.; Sandoz Ltd., Basle; Farbenfabriken Bayer, Leverkusen; and J. G. Geigy S.A., Basle; for supplies of insecticides.

The work was financed from Colonial Development and Welfare funds.

References.

Braithwaite, B. M. (1957). An experiment for the control of bean fly.—*Agric. Gaz. N.S.W.* **68** pp. 95–97.

Ditman, L. P., Cox, C. E. & Kantzes, J. G. (1956). Treatment of pea, snap bean, and lima bean seed with insecticides and fungicides.—*J. econ. Ent.* **48** pp. 688–693.

Hely, P. C. (1948). Bean fly control.—*Agric. Gaz. N.S.W.* **59** pp. 419–420.

van der Laan, P. A. (1949). Over de bestrijding van het katjang-vliegje op kedelee met insecticiden.—*Meded. alg. Proefst. Landb.* no. 98, 28 pp. (*Rev. appl. Ent.* (A) **41** p. 59.)

Moutia, A. (1945). Division of Entomology.—*Rep. Dep. Agric. Mauritius 1944* pp. 14–19.

Moutia, A. (1946). Entomological Division.—*Rep. Dep. Agric. Mauritius 1945* pp. 17–21.

van Someren, G. C. (1956). Notes on the beanfly (*Agromyza phaseoli*) and a trial with insecticidal seed dressing for control.—4 pp. Nairobi, Fison's Pest Control (East Africa) Ltd., 1956.

Starks, K. J. & Lilly, J. H. (1955). Insecticide seed treatment of soybeans in relation to phytotoxicity and seed-corn maggot control.—*J. econ. Ent.* **48** pp. 538–543.

© Commonwealth Agricultural Bureaux, 1959.

THE CONTROL OF ONION FLY, *DELIA ANTIQUA* (MG.), WITH SEED DRESSINGS.

By P. W. Carden *

(Plate XIX.)

Although the onion fly, *Delia antiqua* (Mg.), is not often responsible for crop failures in this country, it causes some losses every year in many places where onions are grown from seed. Experiments carried out by Wright (1938, 1939) suggested that a pure calomel seed dressing or 4 per cent. calomel dust applied to the seedlings in June would control onion fly. However, the cost of these treatments is now very high and in the course of trials designed to find a cheaper substitute it also became apparent that the calomel seed dressing was not very effective. Miles (1955) suggests that the seed dressing was effective in Wright's original trials because of the short time (less than a month) elapsing between his rather late sowing dates and the onion-fly attack, but that calomel is not sufficiently persistent to be effective on crops sown at the normal time—February or March—that is, 2–3 months before the attack commences.

When the chlorinated hydrocarbons became available, McLeod (1946), in Canada, claimed that a seed dressing of 50 per cent. of the weight of seed of pure DDT gave a good control, and that pure calomel weight for weight was also effective, but that the latter delayed germination by a week and checked growth. In the same year, Heringa (1947), working in the Netherlands, stated that DDT at the above rate gave a good control and did not reduce germination, and also that calomel stimulated germination but was not highly toxic to the larvae in the laboratory although it gave good protection in the field. Another Dutch worker, Maan (1947), stated that 40 per cent. of the weight of seed of a 50 per cent. DDT dust was successful and unlike calomel did not reduce germination or growth. Since then several other workers in Europe and North America have recommended DDT, dieldrin, aldrin, heptachlor and parathion used at various rates either as a seed dressing or drilled with the seed.

Methods and Materials.

In 1954–56, trials were carried out on a smallholding on sandy soil at Ridgmont, Bedfordshire, where onion-fly attacks on spring-sown onions have been a serious problem for many years. The normal practice on this holding is to drill variety Giant Orange Zittau at a low seed rate, 4–5 lb. per acre, in mid-March. Hoeing and hand weeding are carried out when necessary but the crop is not thinned. All the trials consisted of five randomised blocks and each plot consisted of three rows, eight yd. long, the rows being one foot apart. Equal weights of seed (*i.e.*, excluding the weight of dressing) were sown in each plot with a hand drill at a depth of 0·5–1 in. within one or two days of being dressed. After drilling, the trials were treated exactly as the grower's crop until they were harvested.

DDT, dieldrin and aldrin were selected as being most promising for comparison with a calomel seed dressing. BHC was not included as it is highly toxic to onions (McLeod, 1946). As seed dressings have several advantages over dusts applied to seedlings, these dust treatments were also omitted.

The materials used were pure calomel, pure DDT and 50 per cent. dieldrin

* Ministry of Agriculture, Fisheries and Food, Anstey Hall, Trumpington, Cambridge.

and aldrin applied as seed dressings. The dieldrin and aldrin seed dressings were prepared from technical material containing not less than 85 per cent. HEOD and not less than 95 per cent. HHDN, respectively. The filler was a siliceous earth. In 1954 and 1955, a small quantity of the wetting agent ' Agral LN ' was mixed with the seed as a sticker before the insecticide was added. In 1956, kerosene was used instead as it is more readily available to the grower.

Counts were made of the number of plants per plot in May and June to show the effect of the treatments on germination, and counts of wilting or dead plants were made once a fortnight while the onion-fly attack was in progress during June and July. The number and weight of onions harvested per plot was recorded.

In periodic checks, nearly all the damaged plants were found to have been attacked by onion fly and no other pest damage was recorded. Miles (1955) has suggested that, on occasions in the past, one of the bean seed flies, *Delia cilicrura* (Rond.), has been confused with the onion fly when attacking onions. There were no examples of *D. cilicrura* among flies bred from several small batches of larvae infesting onions on the site of the trials recorded below. Also, in three seasons, plants showing damage were first seen early in June and fresh damage continued to appear until August which fits in with the life-cycle of onion fly. Thus, it seems certain that the losses of plants which occurred between June and harvest were mainly due to onion-fly attack.

The 1954 Trial.

Calomel was used at the standard rate of 1 lb. calomel to 1 lb. of seed. DDT, dieldrin and aldrin were used at 3·2 oz. active ingredient per lb. of seed (20 per cent. of the weight of seed). Unfortunately, after all the treated seed had been prepared, the seed reserved for the controls was accidentally spoiled and, as it proved impossible to obtain more of the same stock, another stock had to be used for the untreated plots. The germination of the original seed was very poor but that of the replacement seed was much better, so that the figures for the untreated plots in this trial are not comparable with the remainder, but are included to show the level of onion-fly attack and its effect when not checked. As the effect of calomel on the onion-fly attack in this and subsequent trials was very slight, the

TABLE I.

The 1954 field trial (means of five plots).

	Treatments (rate per lb. seed)					Standard error of a single mean
	Control*	Calomel 1 lb.	DDT 3·2 oz.	Dieldrin 3·2 oz.	Aldrin 3·2 oz.	
No. of plants on 5.vii.54 ..	(912)	536	174	436	345	52·3
Damaged plants on 5.vii.54 — No.	(137)	104	0	1	0	—
Damaged plants on 5.vii.54 — Percentage	(15)	19	0	0	0	—
No. onions harvested	(549)	262	171	410	310	—
Percentage loss of plants between 5.vii.54 and harvest	(40)	51	2	6	10	—
Mean weight of onions harvested (lb.)	(59)	29	29	42	46	—

* As a different batch of seed with a higher germination rate was used for the control plots these figures are not strictly comparable with the remainder and are shown in parentheses.

figures for calomel can be regarded as a control for comparison with the other treatments. The seed was sown on 24th March 1954. Plant counts were made on 12th May and 10th June (eight one-ft. lengths of row per plot) and on 5th July (total plants). The relationship between the treatments was very similar in all three counts so only the total plant count is given in Table I.

The germination of the DDT-treated seed was significantly lower than that of the other treatments ($P=0{\cdot}05$). The controls were not included in the analysis.

Plants damaged by onion fly were first seen in mid-June and the attack continued until mid-August with a peak on 5th July when 15 per cent. of the plants on the control plots showed signs of damage. On the calomel plots, with a smaller plant population, the corresponding figure was 19 per cent., but on the DDT, dieldrin and aldrin plots the numbers of damaged plants were negligible.

Owing to the wet summer there were many unripe and thick-necked onions but all the onions were counted and those that were considered marketable were weighed.

The " percentage loss of plants between 5th July and harvest " in Table I was calculated by expressing the difference between the number of onions at harvest and the number of plants on 5th July as a percentage of the latter.

The 1955 Trial.

In view of the serious effect of DDT on germination and possible adverse effects of dieldrin and aldrin, these materials were used in 1955 both at the original rate and at 1·6 oz. active ingredient per lb. of seed (10 per cent. of the weight of seed).

The trial was drilled at 5 lb. per acre on 22nd March 1955, next to the site of the previous trial. Detailed results are given in Table II. Germination was not complete by 6th May on most of the plots but on the aldrin plots a number of plants had disappeared by 10th June. Calomel-treated seed germinated almost as well as the untreated seed. The higher rate of the other materials again reduced germination significantly, but although the reduction by the lower rate of DDT and aldrin was also significant it was less serious. The lower rate of dieldrin appeared to increase germination slightly (significant at $P=0{\cdot}05$).

Onion-fly damage was first noted on the plots in the second week of June. The highest count of damaged plants was made on 21st July when 24 per cent. of the plants on the controls were visibly affected. A view of several of the plots appears in Plate XIX, fig. 1. The beneficial effect of the dieldrin seed dressing is clearly shown.

In September, the onions were pulled and left on the ground to dry for about two weeks and then graded, counted and weighed. On some plots the base of many bulbs had been tunnelled by onion-fly larvae comparatively late in the summer (August), when the plants were large enough to survive the damage (Pl. XIX, fig. 2). This damage had occasionally encouraged splitting or rotting, and it was sometimes impossible to separate this from similar damage due to other causes (weather, disease, etc.) so all unsound bulbs were classed as ' damaged '. Where onion-fly damage was virtually eliminated by treatment, damage due to other causes only amounted to about 2 per cent. The seed coat and remains of the dressing were found persisting among the roots of some onions.

The number of sound and damaged onions harvested per treatment shows the over-all effect of the treatment including that on germination. The effect of the treatment on onion fly is shown better by comparing the number of plants harvested with the plant population on 10th June.

The attack was again very heavy and only 32 per cent. of the plants on the controls were harvested as sound onions.

TABLE II.

The 1955 field trial (means of five plots).

	Treatment (rate per lb. seed)								Standard error of a single mean
	Control	Calomel 1 lb.	DDT 1·6 oz.	DDT 3·2 oz.	Dieldrin 1·6 oz.	Dieldrin 3·2 oz.	Aldrin 1·6 oz.	Aldrin 3·2 oz.	
No. plants 6.v.55	593	558	474	419	630	552	504	447	
No. plants 10.vi.55	607	586	484***	430***	656*	553*	464***	380***	16·5
No. damaged plants on 21.vii.55	143	95	52	13	0	0	0	0	
Percentage damaged plants on 21.vii.55	24	16	11	3	0	0	0	0	
No. sound onions harvested	196	223	275	321	616	510	424	318	
No. damaged onions harvested	108	137	88	45	15	10	4	2	
Total onions harvested	304	360	363	366	631	520	428	320	
Sound onions as % of total plants	32	38	57	75	94	92	91	84	
Damaged onions as % of total plants	18	23	18	10	2	2	1	0	
Plants lost as % of 10.vi.55	50	39	25	15	4	6	8	16	
Weight sound onions (lb.)	26	25	37*	43***	60***	59***	51***	40**	3·0
Weight damaged onions (lb.)	11	13	10	5	1	1	0	0	
Total weight	37	38	47	48	61	60	51	40	
Mean weight per sound onion harvested (oz.)	2·08	1·81	2·14	2·16	1·76	1·84	1·92	1·99	

* Significantly different from control at $P = 0·05$
** ,, ,, ,, ,, ,, $P = 0·01$
*** ,, ,, ,, ,, ,, $P = 0·001$

The 1956 Trial.

Although DDT gave a marked improvement over the controls in 1955 it was not nearly so good as dieldrin or aldrin because of the reduction of germination, so it was not used in this trial. As 1·6 oz. of dieldrin and aldrin had given excellent control, still lower rates were used, 0·5, 1·0 and 1·5 oz. active ingredient per lb. of seed. Calomel was again included. As glasshouse tests had cast some suspicion on the effect of kerosene on germination it was also used alone.

The following materials and rates per lb. of seed were tested in these trials:—calomel (16 oz.), DDT (1·5, 1·6 and 3·2 oz.), dieldrin (0·5, 1·0, 1·5, 1·6 and 3·2 oz.), dieldrin with 5 per cent. or less, by weight, of thiram (see Discussion, p. 806) (0·5, 1·0, 1·5 oz.), aldrin (0·5, 1·0, 1·5, 1·6 and 3·2 oz.), kerosene (5, 12·6, 13·6 and 42 ml.), tractor vapourising oil (5, 12·6 and 13·6 ml.), kerosene with gypsum (13·6 ml.), kerosene with kaolin (12·6 ml.). Dieldrin with thiram was included because some proprietary seed dressings on the market contain the fungicide, thiram (TMTDS).

The trial was drilled on 22nd March 1956. Plant counts made on 7th May and 13th June showed that germination was more or less complete by the earlier date. Although some of the treatments (all of which included kerosene as a sticker) gave improved germination, kerosene, alone, reduced it by 39 per cent. (see below). This was probably the result of using too high a rate of kerosene. Subsequent glasshouse tests showed that 5 ml. kerosene per lb. of seed was effective as a sticker and did not harm germination.

Onion-fly damage was first seen early in June and the highest count of damaged plants was made on 4th July. After harvesting, the onions were counted, graded and weighed as in the previous trial. The attack was again severe—40 per cent. of the plants present on the controls in June disappeared during the summer and nearly half of those harvested were damaged, leaving 33 per cent. as sound bulbs.

Germination.

The field trials showed that some of the treatments seriously impaired germination, so a series of germination trials in a heated glasshouse was undertaken and field trials were also carried out on three other soil types.

In the glasshouse trials, boxes $14\frac{1}{2}'' \times 9'' \times 2\frac{3}{4}''$ of loam were sown with five rows of 20 seeds. Sterilised soil was used in most of the trials. Three boxes were sown per treatment (giving 300 seeds per treatment) and placed on the staging in randomised blocks. The blocks ran parallel to the length of the glasshouse as it had been found that the germination of seeds in boxes nearest the glass was impaired. Counts of seedlings were made at short intervals until maximum emergence.

The additional field trials were on a good, medium sandy loam at Trumpington, Cambridgeshire, a very fine sandy loam at Kirton, Holland, Lincolnshire, and a peaty loam at Manea, Isle of Ely. There was no onion-fly attack on any of these trials.

Percentage germination.

The germination counts from both field and glasshouse trials are summarised in fig. 1. The figures are expressed as a percentage of the germination of untreated seed.

In all trials, calomel-treated seed germinated at least as well as untreated seed. As calomel possesses fungicidal and bactericidal properties its effect on germination compared with untreated seed will depend in part on the fungal and bacterial flora of the soil in which the seed is planted. This may account for the disagreement between various workers on the effect of calomel on germination. Treatment with DDT impaired germination in all trials. The highest rate of dieldrin reduced

TABLE III

The 1956 field trial (means of five plots).

	Treatment (rate per lb. of seed)									Standard error of a single mean
	Control	Calomel 1 lb.	Dieldrin 0·5 oz.	Dieldrin 1·0 oz.	Dieldrin 1·5 oz.	Aldrin 0·5 oz.	Aldrin 1·0 oz.	Aldrin 1·5 oz.	Kerosene 12·6 ml.	
No. plants 7.v.56	390	639***	521***	551***	582***	215***	226***	280***	239***	20·8
No. damaged plants on 4.vii.56 ..	52	49	1	0	2	0	1	0	40	
Percentage damaged plants on 4.vii.56	14	8	0	0	0	0	0	0	17	
No. sound onions harvested ..	123	249	474	517	532	200	200	256	48	
No. damaged onions harvested ..	101	177	34	20	12	7	11	10	63	
Total onions harvested ..	224	426	508	537	544	207	211	266	111	
Sound onions } as % of	33	39	89	93	92	94	91	94	20	
Damaged onions } total plants	27	29	6	4	2	3	5	4	28	
Plants lost } 13.vi.56	40	32	5	3	6	3	4	2	52	
Weight sound onions (lb.) ..	23	29	57***	59***	64***	43***	38**	47***	12*	3·1
Weight damaged onions (lb.) ..	16	20	5	3	1	2	2	1	12	
Total weight	39	49	62	62	65	45	40	48	24	
Mean weight per sound onion harvested (oz.)	3·03	1·86	1·91	1·81	1·91	3·46	3·06	2·95	3·87	

* Significantly different from control at $P = 0·05$
** ,, ,, ,, ,, ,, $P = 0·01$
*** ,, ,, ,, ,, ,, $P = 0·001$

germination by up to 19 per cent. but the lower rates consistently improved germination. The most likely explanation for this improvement seems to be that the dieldrin kills soil arthropods or other small animals which would otherwise damage the seed and also open the way for ' damping-off ' fungi. The inclusion of thiram in the dieldrin dressings did not appear to influence this improvement given by the dieldrin. In most trials all rates of aldrin reduced germination, frequently seriously. Very little stunting or distortion of seedlings was seen, except after treatment with DDT.

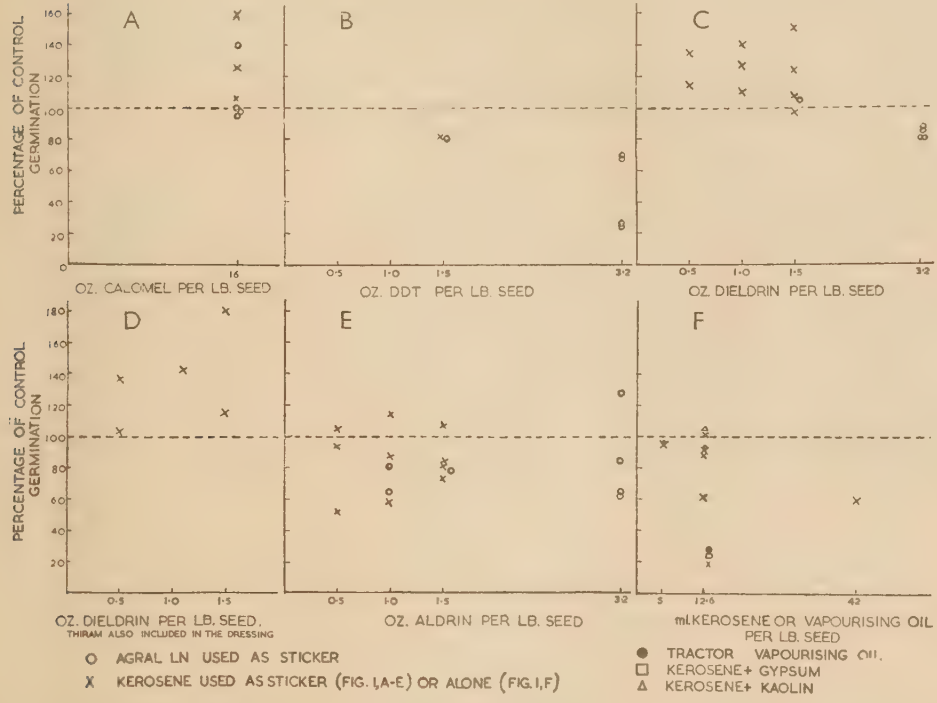


Fig. 1.—The effect of various seed treatments on germination of onion seed. (Field and glasshouse trials.)

In the first glasshouse trial in which domestic kerosene was used as a sticker at 42 ml. per lb. of seed, all the treatments (including kerosene alone) gave unexpectedly low germination counts from seed sown four days after treatment (see fig. 2). However, when some of the same treated seed was sown 20 days after treatment, the counts obtained were normal for those particular treatments (*cf.* fig. 1). It seems probable that the kerosene killed many of the seedlings from the first sowing on germination, but did not damage the dormant seed. By the second and subsequent sowings, much of the kerosene would have vaporised and consequently the seedlings were able to survive. In later trials, kerosene as a sticker was used at much lower rates (5, 12·6 and 13·6 ml. per lb. of seed) and normal counts were obtained for the various insecticidal treatments, but kerosene alone, at 12·6 and 13·6 ml., reduced germination, to a variable extent, in all trials (fig. 1, F). It is thought that, in the presence of the insecticidal seed dressing,

the kerosene was absorbed by the latter, so kerosene was also tried with dressings of non-insecticidal materials. Seed treated with kerosene plus kaolin germinated as well as untreated seed, but treatment with kerosene plus gypsum, which is less absorbent than kaolin, was no better than treatment with kerosene alone. In a single glasshouse trial, seed treated with kerosene alone at 5 ml. per lb. of seed germinated as well as the untreated seed. Tractor vapourising oil gave similar results to domestic kerosene.

Retardation of germination.

There was no suggestion in the field trials that any of the treatments retarded germination, and at Manea all three rates of dieldrin-thiram dressing appear to have had the opposite effect. However, in the glasshouse, several treatments appear to have retarded germination in some trials but not in others. This effect seems to have been confined to treatments or trials where the total germination was low because of the effect of the treatment, unfavourable conditions or weak seed.

Variability of results under different conditions.

Various workers have expressed different views on the effect of seed dressings on the germination of onion seed and comparison of the three field trials in 1956 (Table IV) shows that the effects varied considerably even on fairly similar soil types in the Eastern Counties in the same season. One possible explanation of the conflicting results obtained by different workers is that different stickers have been used, which have had different effects on germination. However, in each of the above trials the sticker was kerosene, so it is obvious that there is some other factor or factors involved, such as climate, soil type or soil fauna and flora. For this reason it is important to use only the minimum amount of material that will give satisfactory control of the pest, because although the material may be harmless to the crop on one soil, on another it may reduce germination.

TABLE IV.

The effect on germination of seed dressings at different sites in 1956 (means of five plots).

	Soil type	Treatments (rate per lb. seed)								
		Control	Calomel 1 lb.	Dieldrin 0·5 oz.	Dieldrin 1·0 oz.	Dieldrin 1·5 oz.	Aldrin 0·5 oz.	Aldrin 1·0 oz.	Aldrin 1·5 oz.	Kerosene 12·6 ml.
Ridgmont	Sandy	100	164	134	141	149	55	58	72	61
Trumpington	Medium sandy loam	100	104	—	113	111	95	88	84	90
Kirton	Very fine sandy loam	100	126	116	128	126	103	115	106	88

Germination expressed as a percentage of the control germination.

Storage of treated seed.

Wright (1939) found that seed treated with calomel could be stored safely in wooden, cardboard or paper containers without affecting viability but that, if the seed was placed in a closed glass or metal container, viability fell rapidly and the whole sample was killed within 10–16 weeks. In order to find whether the viability of seed treated with the chlorinated hydrocarbons was similarly affected,

samples of seed were treated with DDT, dieldrin or aldrin at 1·5 oz. active ingredient per lb. of seed using kerosene as a sticker. Part of each sample was placed in an unsealed packet and the remainder in a corked tube. Sowings of 3 × 100 seeds per treatment were made 4, 20, 35 and 74 days after treatment.

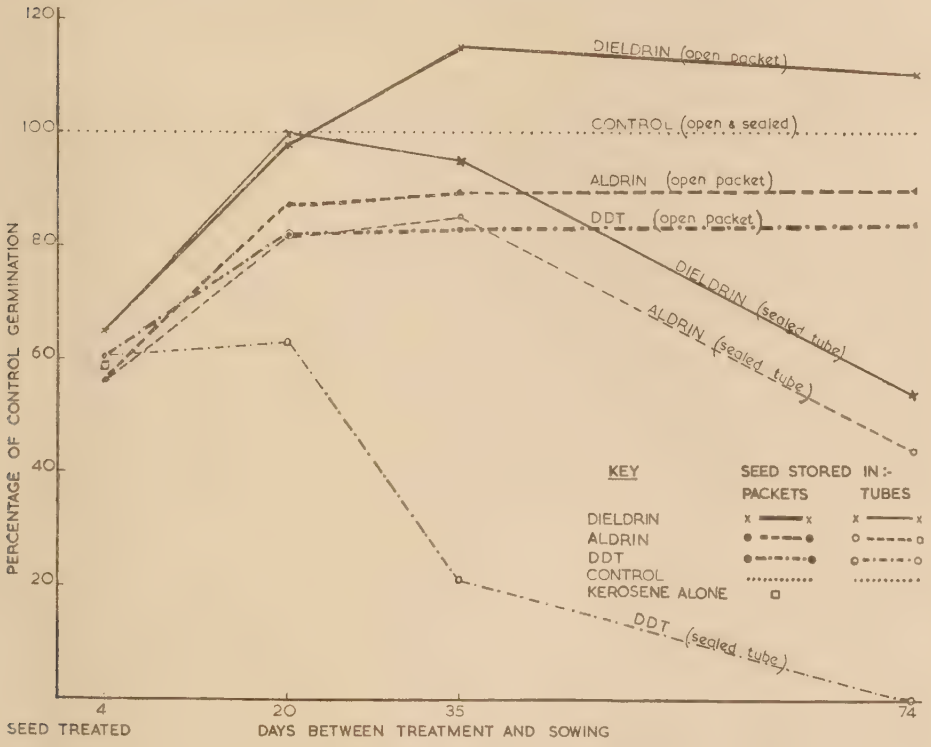


Fig. 2.—Germination of onion seed stored after treatment. All dressings were applied with kerosene as a sticker.

The germination of the untreated seed was 78 per cent. at the first sowing but after that remained steady in the range 60–66 per cent. whether stored in packets or tubes. At the first sowing, the germination of the seed treated with each insecticide was very low, perhaps because too much kerosene was used, as suggested above, but at the subsequent sowings up to 10½ weeks after treatment, the seed from the packets treated with each insecticide gave normal counts (fig. 2). However, the germination of the seed that had been stored in closed tubes after treatment with DDT remained constant at the second sowing and fell rapidly after that. The germination of the seed treated with dieldrin and aldrin and stored in tubes was as good as that stored in open packets at the second sowing but fell after three and five weeks, respectively. It appears from this that it is safe to keep treated seed for at least one or two months provided that it is not stored in an airtight container. (This may not apply to large batches.)

Other Materials for Use as Stickers.

Starch paste made up at 3 teaspoonfuls of flour to ½ pint water, and 4 per cent. methyl cellulose solution, have also been used as stickers. They both appear

satisfactory provided that the correct quantity of each material is used for the rate of insecticide. The most satisfactory method of application was found to be to add the sticker to the seed and stir it in thoroughly. The insecticide was then added and stirred in until evenly distributed. Shaking alone was not satisfactory when treating small batches of seed. The treated seed should be allowed to dry fairly quickly.

Discussion.

Examination of yield figures in the three main trials shows that there were two factors affecting yield—the level of onion-fly attack and the initial plant population. The onion-fly attack was more important, but at a given level of attack the yield was dependent on the plant population, although the effect of this was reduced to some extent by the lower populations producing larger onions. There was close correlation between the yield per 100 plants in the original stand and the percentage of plants attacked by onion fly. Analysis of the three years' figures, after angular transformation of the percentage of attacked plants, gives a correlation coefficient $r = -0{\cdot}842$ (significant at $P = 0{\cdot}001$). In fig. 3, the scatter of the 1954 and 1955 points suggests a straight-line relationship between the yield and percentage attack although in 1956 there was an indication that a curve would fit the points better. As this only applied to the one year, straight trend lines have been calculated for each year's figures. The regression coefficients for 1954 and 1956 are very close but that for 1955 is appreciably but not significantly different. If this is a true difference it may be a reflection of the unusually hot,

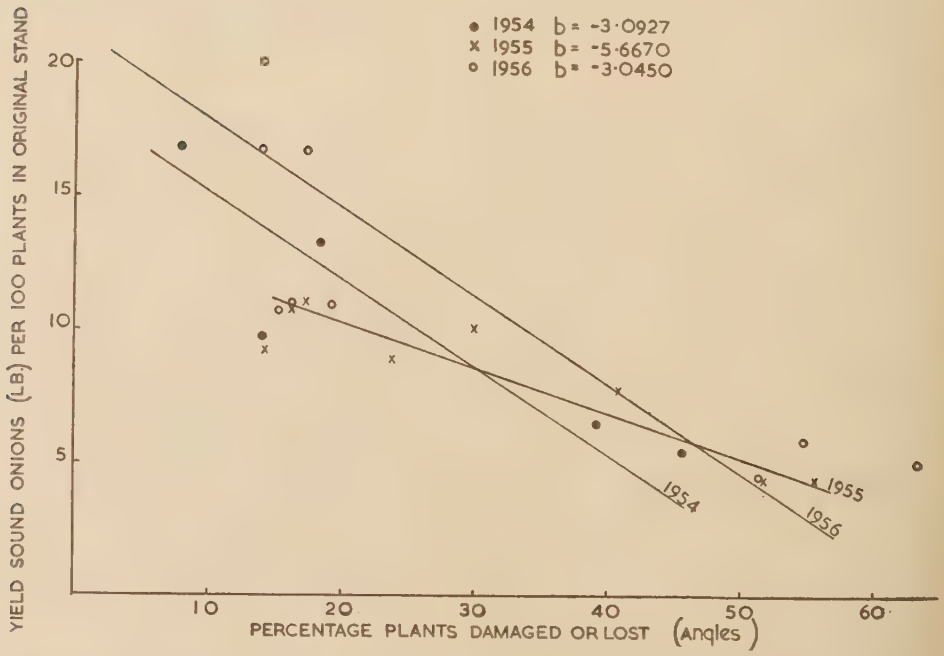


Fig. 3.—The effect of onion-fly attack on yield per 100 plants in original stand.

dry summer in 1955. It appears from the original figures for the three years that for every 10 per cent. plants attacked the yield was reduced by about 10 per cent.

It will be seen from Tables I–III that even where 60 to 70 per cent. of the plants were damaged or destroyed during the season the most plants showing damage at any of the fortnightly counts ranged between 8 and 24 per cent. It seems likely that the true level of onion-fly attack is frequently under-estimated because of the difference between the number of obviously attacked plants and the true level of attack.

The calomel seed dressing did not give any marked reduction of the onion-fly attack in any of the trials and, although it improved germination over the control by over 60 per cent. in 1956, this only resulted in a 26 per cent. increase in yield of sound onions. Other workers have also encountered this failure of calomel to control onion fly. In Canada, McLeod (1946) found that a calomel seed dressing gave only partial control of onion fly although he was working on a crop grown for sets which was sown on 21st May so that the time between sowing and the onion-fly attack was probably short. Finlayson & Handford (1954), Jørgensen (1955) and Finlayson (1957) also found that it did not give a satisfactory control. Maan (1947) suggested that calomel controlled the secondary attack but did not control the primary attack which is of less importance. This does not appear to have happened in the Bedfordshire trials. Calomel is, however, still accepted as effective against white rot (*Sclerotinia cepivora*) (Croxall, Sidwell & Jenkins, 1953; Wiggell, 1956).

DDT gave a marked increase in the weight of sound onions in spite of much smaller plant populations. In 1954, when there was little late summer damage to the bulbs on the controls (*i.e.*, few of the onions harvested had any onion-fly damage to the base), there was no onion-fly damage on the DDT plots, but in 1955 when there was heavy late summer damage on the controls, there were many damaged bulbs on the DDT plots. Comparison of the percentage of damaged onions harvested with the percentage of damaged plants present on 21st July suggests that DDT greatly reduced the early attack but was not sufficiently persistent to prevent the later damage. It is evident, from the lower rate of dressing, that a rate which did not upset germination would be too low to prevent a serious attack by onion fly.

As was to be expected, kerosene alone had no effect on onion fly, and only 20 per cent. of a small initial plant population reached maturity as sound onions.

As dieldrin and aldrin both gave an excellent control of onion fly at all rates, the yields from seed treated with these materials were largely a reflection of the initial plant population apart from the tendency of the lower populations to produce larger bulbs.

In 1955, in addition to the serious reduction of germination by both rates of aldrin, many plants disappeared from the plots between the first plant count and harvest in spite of the lack of onion-fly damage (see Table II). Comparison of the first and second plant counts (6th May, 10th June) shows that about half the losses occurred before the onion-fly attack commenced, so it seems possible that they were due to a delayed phytotoxic effect of the aldrin. Evidence which may be relevant is given by Walz (quoted by Finlayson, 1957), who states that 2 lb. aldrin per acre applied to the furrow with onion seed did not hamper germination but altered cellular development of the seedling roots and that recovery was slow in plants that survived the treatment. Losses after treatment with aldrin in 1954 were also slightly higher than might have been expected, but those in 1956 were not. Examination of the relevant rainfall figures does not show any relationship between phytotoxicity and rainfall.

In both 1955 and 1956, all the dieldrin treatments yielded more than double the weight of sound onions harvested from the controls. Dieldrin at 3·2 oz. per lb. of seed slightly reduced germination but there were no significant differences

between the other rates. Losses of plants from the dieldrin plots were very low in all the trials.

The results of these trials suggest that the most satisfactory material for use as a seed dressing to control onion fly is dieldrin. In view of the possible risk of adverse effects on germination on different soils or under different climatic conditions, and also the cost of the material, the lowest rate, 0·5 oz. actual dieldrin per pound of seed, is probably most suitable. Besemer & van de Vliet (1956) state that a DDT seed dressing gives less protection on humus soils than on other soils, as is the case with seed dressings used against carrot fly on carrots. Therefore, it might be advisable to use up to 1·5 oz. actual dieldrin per lb. of seed on soils containing a high percentage of organic matter. The trial on peaty loam at Manea was designed to provide information on this point but there was no attack by onion fly.

Dieldrin-thiram dressings, similar to the proprietary materials on the market, improved germination by about the same percentage as the corresponding rates of dieldrin alone. Thiram may give some protection against 'damping-off' (*Pythium* spp.) but will not affect white rot and is not likely to control onion smut (*Urocystis cepulae*) at this low rate (*cf.* Larson & Walker, 1953).

The cost of a proprietary dieldrin-thiram seed dressing at 0·5 oz. actual dieldrin per lb. of seed (or about 0·75 oz. of 75 per cent. material) and 6 lb. of seed per acre is 12*s.* 6*d.* per acre (in 1958). In comparison, treatment of 6 lb. of seed with an equal weight of pure calomel would cost about £8 for material, and application to the rows of 4 per cent. calomel dust at about 3 cwt. per acre would cost about £35 plus the cost of application.

Summary.

Seed treatments of calomel, DDT, dieldrin and aldrin were compared in three seasons' field trials for use against onion fly, *Delia antiqua* (Mg.). Excellent control and also improved germination were obtained with 0·5 oz. actual dieldrin per lb. of seed applied with a sticker, with or without thiram. Similar results were obtained with 0·1 and 1·5 oz. actual dieldrin per lb. of seed, but 3·2 oz. reduced germination. Aldrin at the same rates gave excellent control but reduced germination. DDT at 1·5 oz. and 3·2 oz. gave good control early in the season, but was not sufficiently persistent and seriously reduced germination. Calomel gave little control, although it improved germination.

Although kerosene used as a sticker for a dust was satisfactory, it was liable to reduce germination seriously when used alone, except at very low rates.

Seed treated with DDT, dieldrin or aldrin may be stored safely for a month or two in unsealed containers but not in sealed containers.

There was close correlation between the percentage of plants attacked and the yield per 100 plants in the original stand. For every 10 per cent. of plants killed by onion fly there was a 10 per cent. loss of the potential yield.

Even where the onion-fly attack was heavy, comparatively few plants showed symptoms of damage at any one time, which suggests that the level of attack is frequently under-estimated.

Acknowledgements.

I am very grateful to Dr. H. C. Gough for his advice at all stages of the work, and to other members of the National Agricultural Advisory Service for their help with the field work, to Messrs. R. Barnwell, Ridgmont, Beds., and S. H. Guy, Manea, Cambs., for providing sites for field trials, to the Shell Chemical Company for providing the aldrin and dieldrin seed dressings, and to Mr. W. E. Dant for taking the photographs.

References.

BESEMER, A. F. H. & VAN DE VLIET, M. (1956). Bestrijding van de uievlieg, *Chortophila antiqua* Mg. door een zaadbehandeling met gechloreerde koolwaterstoffen.—*Versl. PlZiekt. Dienst Wageningen* no. 129 pp. 172–176.

CROXALL, H. E., SIDWELL, R. W. & JENKINS, J. E. E. (1953). White rot (*Sclerotium cepivorum*) of onions in Worcestershire with special reference to control by seed treatment with calomel.—*Ann. appl. Biol.* **40** pp. 166–175.

FINLAYSON, D. G. (1957). Further experiments on control of the onion maggot, *Hylemya antiqua* (Mg.), in the interior of British Columbia.—*Canad. J. Pl. Sci.* **37** pp. 252–258.

FINLAYSON, D. G. & HANDFORD, R. H. (1954). Experiments on control of the onion maggot, *Hylemya antiqua* (Meig.) in the interior of British Columbia.—*Canad. J. agric. Sci.* **34** pp. 385–388.

HERINGA, J. W. [?1947]. Onderzoek naar een vervangingsmiddel voor calomel ter bestrijding van de uienvlieg.—*Rep. 1st int. Congr. Pl. Prot.* pp. 337–350.

JØRGENSEN, J. (1955). Løgfluen, *Hylemyia antiqua*, Meig. Resultater af nogle biologiske undersøgelser og bekaempelsesforsøg.—*Tidsskr. Planteavl* **59** pp. 252–279.

LARSON, R. H. & WALKER, J. C. (1953). Thiram for smut control in onion set plantings.—*Phytopathology* **43** pp. 596–597.

MAAN, W. J. (1947). Zaadbehandeling met D.D.T. tegen de uienvlieg.—*Tijdschr. PlZiekt.* **53** pp. 11–13.

MCLEOD, W. S. (1946). Hexachlorocyclohexane in the control of onion maggot.—*J. econ. Ent.* **39** pp. 631–637.

MILES, M. (1955). Studies of British Anthomyiid flies. VII. The onion-fly complex.—*Bull. ent. Res.* **46** pp. 21–26.

WIGGELL, D. (1956). Control of white rot in onions.—*Plant Path.* **5** pp. 60–61.

WRIGHT, D. W. (1938). The control of the onion fly.—*J. Minist. Agric.* **44** pp. 1081–1087.

WRIGHT, D. W. (1939). The control of onion fly (*Delia* (*Hylemyia*) *antiqua* Meig.).—*Agriculture* **46** pp. 147–154.

© Commonwealth Agricultural Bureaux, 1959.



FIG. 1. Control of *Delia antiqua:* a view of part of the 1955 trial. Foreground, seed treated with aldrin; mid-ground, seed untreated; background, seed treated with dieldrin.



FIG. 2. Harvested onions showing damage to the base caused by larvae of *Delia antiqua.*

SOME RECENT OBSERVATIONS ON *BUSSEOLA FUSCA* (FULLER) (LEP., NOCTUIDAE) IN SOUTHERN RHODESIA.

By C. N. Smithers

Entomological Branch, Federal Ministry of Agriculture, Southern Rhodesia.

Jack (1917) indicated that *Busseola fusca* (Fuller), the maize stem borer, is the most serious maize pest in Southern Rhodesia and estimated a loss of 75 per cent. of the crop due to activities of the second-generation larvae. Swaine (1957) obtained an increase of 83 per cent. in the yield of maize cobs on African-owned plots in Tanganyika by the application of insecticides. In South Africa, du Plessis & Lea (1943) assessed the loss at about 10 per cent. There have been no critical investigations into maize losses from *B. fusca* in the Federation of Rhodesia and Nyasaland but it is quite unlikely that increases of the order recorded by Swaine could be obtained on European-owned land, on which the present observations have all been made. The situation on African-owned land is even less well-known.

The degree of infestation of plants varies from practically nil to almost 100 per cent. Counts made in February 1956 in the Salisbury area indicated that an average of 92 per cent. of the plants were infested on untreated lands and that each plant contained an average of 2·18 apparently healthy pupae.

The observations on which this paper is based were made in order to fill some of the gaps in our knowledge of this important insect under Rhodesian conditions and to obtain fuller data on some little-known aspects of its biology. Jack (1917) and Mally (1920) should be consulted for general accounts of the species in southern Africa. These authors list the food-plants known from Southern Rhodesia and South Africa, respectively, and Jepson (1954) lists food-plants generally. Jack (1917) mentions *Pennisetum purpureum* as a food-plant, but the common species of borer (the larvae of which cannot be distinguished at present from those of *B. fusca*) reared from this plant by Mr. D. J. W. Rose has been described by Bowden (1956) as *Busseola phaia*. Great care, therefore, should be exercised in identifying borer larvae from *P. purpureum* and for certain determination it is necessary to rear larvae through to the adult stage, as both species are known from *P. purpureum* in Southern Rhodesia. *B. phaia* has not yet been reared from maize.

The Egg Stage.

As will be shown later, there are only two main generations a year, the first of which passes through its development without a break, whereas most individuals of the second generation pass the dry season as fully fed larvae in a state of diapause.

Details of the length of the egg stage in the two main generations, in the laboratory and in field cages, are given in Table I.

After mid-December, there was a noticeable shortening in the length of the egg stage of the first generation in the laboratory. Unfortunately, the field-cage eggs for this period were accidentally destroyed, but the shortening was evident in the second-generation eggs (laid after mid-February) in both field and laboratory.

Eclosion is by the usual Noctuid method of biting through the chorion. Usually most of the chorion is left; the exit hole is normally towards one side of the egg.

TABLE I.

Length of egg stage (in days) of *Busseola fusca* in Southern Rhodesia.

Period during which eggs laid	In laboratory			In field		
	Total eggs laid	Length of egg stage		Total eggs laid	Length of egg stage	
		Range	Mean		Range	Mean
30.x.56—14.xii.56 ..	1070	8–13	10·3	1552	11–13	11·4
19.xii.56—11.i.57 ..	872	8	8·0	—	—	—
14.ii.57—1.iii.57 ..	2100	7–9	7·7	3897	7–8	7·3

The Larval Stage.

Number of moults and duration of instars.

Details of the lengths of larval instars in the first generation are given in Table II. These figures exceed those given, for Tanganyika, by Swaine (1957).

TABLE II.

Duration (in days) of larval instars in the first generation of *B. fusca*.

	Instars						
	1	2	3	4	5	6	7
Average duration of instar	6·5	4·0	3·2	4·0	4·8	13·9	15
Range	4–8	3–5	2–7	2–5	3–7	11–18	—
No. of individuals ..	34	26	20	16	14	10	1

Mean length of larval life: 36·8 days
Range : 33–42 days

Of the first-generation larvae reared in the laboratory, only one entered a seventh instar prior to pupation; the usual number of instars appears to be six, but, in the second generation, diapause larvae may undergo one or two extra moults without any appreciable change in size or activity.

In larvae of the second generation, variations in length of the later instars are considerable, whether or not they enter diapause; this is probably due, in the main, to the variable condition of the food available to that generation.

Variation in the date of entry into diapause is also very considerable, but by mid-June the bulk of the larvae in the field that will survive are in diapause and the majority of these pupate in early November.

Feeding habits.

When larvae of the first generation hatch, in November–December, they are usually on comparatively small and immature plants. After hatching, they remain on the egg-mass for anything up to 24 hours, after which most of them climb to the top of the plant and enter the funnel, where they commence feeding on the most tender leaves; some climb to the uppermost parts of leaves and may be wafted from there on to neighbouring plants, which they attack by way of the funnel. Where the eggs have been laid on very small plants, a few larvae may feed on the tissues of the leaf sheath under which they have hatched or they may, exceptionally, bore directly into the soft internal tissues. All larvae, of course, finally enter the stem. Larvae that do not commence their feeding in the funnels of the plants, however, constitute but a small percentage of the total. Young larvae have not been observed mining in the midrib of leaves, as recorded by Ingram (1958). In the laboratory, newly hatched larvae have lived for three days without food; in the field, it is possible for them to be wafted a considerable distance during this period, although observed infestation patterns on fields of young maize suggest that comparatively little movement of newly hatched larvae takes place.

When larvae of the second generation hatch, in February–March, their behaviour pattern is essentially that of the first generation, but the maize plants are older, larger and more mature. Those larvae that climb to the top of the plant commence feeding on the soft tissue of the upper leaves; others find their way down between the upper leaf sheaths, into the silk or tassel, or under the cob sheaths. Those on the silk and under the cob sheaths frequently find their way into the more or less developed cob and eventually into the stem after damaging the cob. There is, in fact, a tendency for young larvae at this time to accumulate in the silk and under cob sheaths, a process which has given rise to an erroneous belief that the moths at this time show a preference for laying on the developing cobs. The author has found no evidence for such a belief and the great majority of eggs laid at this time are to be found, as usual, under the leaf sheaths of the plants. Difference in feeding activities in the different stages of the crop are directly attributable to the state of the plants at the time, and to the initial positively phototropic reaction of the larvae which later become negatively phototropic. Generally, leaf tissue only is eaten until about the third instar (exceptionally, soft stem tissue may be taken) after which the larvae become capable of attacking the harder stem tissue. In most cases where young larvae had apparently been boring within the plant, close inspection usually revealed that they had, in fact, attacked mainly the closely rolled leaves and leaf sheaths.

Young larvae live in and bore through the frass made by their own massed efforts in the funnel. Larger larvae, in individual burrows in the stems, throw out the frass when the burrow is short, but merely compact it when the burrow is longer, thus maintaining a length of clear burrow.

Preparation for pupation.

Prior to pupation, the larvae increases the diameter of the burrow and bites away the plant tissue from the inside of a small portion until only the thin 'window', mainly of epidermal tissue, remains between it and the exterior. It then retreats a short distance along the tunnel. In many cases, but not all, a certain amount of loose webbing is spun, in which may be incorporated frass particles; this forms a very flimsy cocoon. Frequently the amount of spinning is negligible. In the laboratory, very few larvae pupated within the stems; most of them did so between loose leaves in the glass breeding tubes after constructing a very loose cocoon of silk and frass. The elaboration of the structure under such conditions varied considerably.

An interesting difference in larval behaviour between Southern Rhodesia and

South Africa was noticed. The habit shown in South Africa by diapause larvae of retiring to the lowest parts of the stem for diapause and pupation is not at all marked in Southern Rhodesia. The distance above ground at which diapause larvae were found was measured in more than 200 stems on the Salisbury Experiment Station. In these, only 23 per cent. of the larvae occurred in the lowest 10 in. of the plant, and only 8 per cent. below 7 in., while 36 per cent. occurred at between 10 and 20 in. The extent to which larvae retire to the lowest part of the stem for pupation appears to depend on local conditions, probably mainly temperature.

The Pupal Stage.

Data on the length of the pupal stage in the first and second generations for the Salisbury area are given in Table III.

TABLE III.

Length of pupal stage in *B. fusca* (in days).

Generation	No. of pupae	Mean	Range
I	96	16·6	14–26
II	125	23·1	18–33

The data given in Table III were obtained from larvae collected in the field and allowed to pupate in the insectary. Pupations were recorded daily. Data on the second-generation pupae were obtained during November and December, those for first-generation pupae during late January and February.

The Adult.

Variation in size.

The size of moths, particularly in the second generation, varies greatly, presumably according to larval feeding, but without apparently affecting their fecundity or fertility.

Food of moths.

In the breeding cages, the moths were usually provided with sugar water or diluted honey on cotton-wool pads held in small dishes or glass tubes. Moths of both sexes were seen to be resting on or near these substances, but without feeding, and where they were not provided, egg-laying appeared in no way impaired. Mally (1920) records that a moth was seen to imbibe dew after being confined in a dry cage for some days.

Activity of moths.

Moths caged over large maize plants in the open passed the daylight hours on the ground and not on the plants. A large number was observed over a period of six days and they were found during the day under clods of earth and in leaf litter on the ground or resting on the soil; occasionally one was found on the wire gauze of the cage. All the resting places likely to be available to the moths in the field were available in the cages and it is not likely that the behaviour of the moths differed from their normal field behaviour. Oviposition of fertile eggs continued normally.

From observations in the laboratory and in field cages it seems that the males are far more active than the females. Males were very often observed in flight at night and soon became tattered and rubbed in captivity; whereas females, although they would sit for long periods vibrating their wings were seldom seen in flight and retained a fresh appearance until death. The greater activity of the males may be responsible for their preponderance over females in light-trap catches, since it makes their entry into the area influenced by the light more likely.

The record of catches in the mercury-vapour light-trap at the Salisbury Experiment Station from 7th February 1955 to 4th April 1957 is given in Table IV. The trap was in operation from 4th January 1955. In the records, sexes are not always distinguished but in those cases where they have been, the ratio of males to females trapped was 5 : 1.

TABLE IV.

Record of captures of *B. fusca* in mercury-vapour light-trap at Salisbury Experiment Station, S. Rhodesia.

Year	Month						
	i	ii	iii	iv	v–x	xi	xii
1955 ..	0	35	36	4	0	0	0
1956 ..	1	17	22	5	0	3	4
1957 ..	1	21	64	2	—	—	—

It will be noted that during six months of the year no moths were caught, and that the number captured that could be regarded as representing the diapause generation was very small, namely, the seven caught in November–December 1956. All the rest were of the first generation. Three factors are probably responsible for this. First, owing to high mortality of larvae of the second generation, both before and during diapause, the number of moths available for capture is relatively small. Secondly, on the Salisbury Experiment Station, maize plants are always removed from most of the lands fairly soon after harvesting and certainly some weeks before the diapause larvae pupate. The Station lands themselves, therefore, are unlikely to be the source of many moths of this generation. Thirdly, as the Experiment Station is surrounded mainly by non-agricultural lands, the number of invading moths must be very limited.

There is little doubt that females can and do fly long distances when necessary but, from the behaviour so far observed, it seems unlikely that they do so if males, and plants suitable for oviposition, are available. In any case, it is the males that are more active and they would probably be attracted to the females. In the field, groups of infested plants are often found at some distance from similarly infested groups (especially in light infestations). This may be due in some measure to the limited range of the individual female, which will result in oviposition on a group of adjacent plants. The extent of each infested group may be somewhat enlarged by the movement of newly hatched larvae.

Length of adult life.

The length of life of moths kept in large wire cages over maize plants is shown in Table V. The females concerned laid fertile eggs whilst under observation.

The length of adult life shows considerable range, but little difference in mean value between the two generations or the two sexes.

Sex ratio.

Of 287 reared moths of which the sex was recorded, 140 were females and 147 males; the sex ratio, therefore, may be taken as 1 : 1.

TABLE V.

Length of life of adults of *B. fusca*.

Origin of moths	Time of emergence	Sex	No. of moths observed	Length of life (days)	
				Range	Mean
Diapause larvae	Late November, 1956	M	17	2–11	6·4
		F	22	3–12	7·6
Non-diapause larvae	Late February, 1957	M	9	4–9	6·7
		F	12	4–12	7·1

Copulation.

Both males and females are ready for copulation almost as soon as they have emerged. In the laboratory, males and females were confined in pairs in cages the morning after emergence. In some cases, fertile eggs were laid the following night, indicating that females are capable of mating successfully and ovipositing within 24 hours of emergence. Data given below show, for a total of 29 female moths (17 from diapause larvae and 12 of the first generation) the number of days then elapsing before the first batch of viable eggs was laid:

Days to first batch	0	1	2	3	4	5
No. of females laying first batch	5	12	6	4	1	1

Moths of the two generations did not differ.

Although eggs may be laid by virgin females they do not hatch. In the laboratory, such eggs were seldom laid within four days of the females' emergence, and all collapsed within a few days of laying. The laying of viable eggs is therefore taken to indicate that successful copulation has taken place.

As females which were allowed males for only one night did not lay appreciably fewer viable eggs than females constantly accompanied by males, it would seem that one mating is sufficient. Some males are capable of at least four successful matings, and, of eight tested in February 1957, all mated at least twice, the dates of successful matings (expressed as the number of days elapsing since the emergence of the male) being as follows: 1, 3, 4; 1, 2, 3; 1, 4, 8; 1, 2, 3, 5; 1, 7; 1, 4; 1, 5; and 1, 4.

Reproductive capacity of females.

Data on the egg-laying activities of females caged in the laboratory over potted maize plants are given in Table VI. The number of eggs in each batch is shown, the nights on which laying took place being numbered consecutively from that on which oviposition first took place. The day of death of the female is indicated by ×. The great variation in egg-laying capacity and the period over which oviposition is carried out are noteworthy. Several days may pass between the cessation of egg-laying and death.

The diameter of the stem of the plant affects the size of the egg-batch to some extent. In smaller plants there are fewer longitudinal rows to the batch than in larger plants.

TABLE VI.

Reproductive capacity of females of *B. fusca*.

Moths from diapause larvae	Days of laying and batch sizes											No. of batches	Period of laying (days)	Total eggs per female
	1	2	3	4	5	6	7	8	9	10	11			
1	45, 54	83, 46, 59, 53	22, 59	9, 14, 31	47, 33						×	13	5	555
2	108, 85, 15	17	106, 20				×					6	3	351
3	298, 23	79, 9	21, 36	51	9	27, 16		×				10	6	569
4	6	86	×									2	2	92
5	141, 93, 14, 10	66	48	9		23, 8			31, 4, 24	×		14	9	536
6	34	23, 30			×							3	2	87
7	102, 371			27	×							3	4	500
8	25, 60								×			2	1	85
9	49		87	71		×						3	4	207
10	107		184, 17	27, 8		39	×					6	6	382
11	106, 38		14	213	40,	8			×			6	6	419
12	73	99	78, 114		×							4	3	364
Average ..	..	..	..	..	..	..	..	..	..	..	..	6·0	4·2	345·5
Range ..	..	..	..	..	..	..	..	..	..	..	..	2–14	1–9	85–569

Moths from non-diapause larvae	Days of laying and batch sizes											No. of batches	Period of laying (days)	Total eggs per female
	1	2	3	4	5	6	7	8	9	10	11			
1	12						×					1	1	12
2	3	76	152		40, 23		×					5	5	294
3	20	13, 26		14	31	24		×				6	6	128
4	40, 30	36	×									3	2	106
5	21	336	×									2	2	357
6	27, 51, 94, 144	56, 179, 105	51	206	19		×					10	5	932
7	263, 364	161	139	31	41	×						6	5	1032
8	13, 36, 21, 9, 160	24, 30	240, 16, 36	42	44	×						12	5	671
9	98	56	28		×							3	3	182
10	22, 19	4				×						3	2	45
11	56, 206	66	49		×							4	3	377
Average ..	..	..	..	..	..	..	..	..	..	..	..	5·0	3·5	376·0
Range ..	..	..	..	..	..	..	..	..	..	..	..	1–12	1–6	12–1032
Over-all average	..	..	..	..	..	..	..	..	..	..	..	5·5	3·9	360·0

× indicates day of death.

Effects of Food Supply and Food Condition.

Generally, the activities of *B. fusca* are so adjusted that food shortage is not an important factor under normal farming conditions. The condition of the food available, however, has an important bearing on larval physiology and activity. The present studies have shown that larvae fed on young terminal sections of maize stem or on young developing cobs grow quicker than do those fed on other parts of the plant. It is possible to rear *B. fusca* continuously in the laboratory on fresh green maize-plant tissue; the larvae develop rapidly and pupate without any indication of a late-instar larval diapause. In the field, however, the bulk of the late-instar larvae that are still feeding as the maize stems dry out go into a diapause, which persists throughout the dry season and does not end until the rains start, late in the year.

Parasitism by *Sturmiopsis parasitica* (Curr.).

The Tachinid, *Sturmiopsis parasitica* (Curr.), is the commonest parasite of *B. fusca* in the Salisbury area and appears to be the only one that occurs in large numbers. Details of its incidence on larvae of both generations from localities at and near Salisbury during 1956 and 1957 are given in Table VII. Of

TABLE VII.

Incidence of *Sturmiopsis parasitica* in larvae of *B. fusca*.

Generation	Locality	Date	No. collected	No. parasitised	%
I	Near Salisbury	12–13.ii.57	275	98	35·6
II	Gwebi College	1.v.56	283	13	4·6
	Gwebi College	7.v.56	83	3	3·6
	Salisbury	21.vii.56	33	9	27·3
	Salisbury	25.vii.56	368	123	33·4
	Salisbury	2.viii.56	50	4	8·0

the parasitised larvae, about 65 per cent. yielded one adult fly, 21 per cent. yielded two flies, 10 per cent. yielded three and 4 per cent. yielded four flies.

Cannibalism.

Under the congested conditions that arise in the funnels and upper stems of small maize plants, cannibalism may occur amongst the larvae of *B. fusca*. For this reason, only relatively small numbers can be placed together in one length of stalk in the laboratory; this applies particularly to larvae in the earlier instars. The extent of cannibalism in the field is not known, although under crowded conditions it could certainly be an important factor in larval mortality.

Diapause.

Observations in the field and laboratory suggest that the drying out of the maize plant is of some importance in inducing diapause and this is confirmed by the fact that successive non-diapause generations may be reared continuously on fresh green food. In Salisbury, attempts to induce pupation in diapause

larvae by chilling for various periods and by maintaining the larvae in 15-hour light periods were unsuccessful. Swaine (1957) succeeded in inducing pupation by placing and keeping diapause larvae in contact with water.

Larvae in diapause are normally inactive, but are capable of much movement if necessary. If removed from their stalks they will start to excavate new burrows immediately.

In the Salisbury area the majority of diapause larvae pupate in the field in late October or early November. It should be pointed out that not all larvae of the second generation do, in fact, enter diapause (see below), whilst in some examples the period of diapause is considerably shortened. This leads to the formation of pupae and the emergence of a few moths at almost any time during the dry season. Pupae have been collected during July and August, and it may be surmised that these are from larvae that have reached a sufficiently advanced stage of development before the food becomes too dry for feeding.

Résumé of the Seasonal Cycle.

In discussing the seasonal cycle of *B. fusca* in Rhodesia it is best to start with the situation as it is in normal farmland at the end of the dry season, just before the main rains commence, that is, in mid-October. At this time the bulk of the borer population is in diapause as late-instar larvae. With the onset of the rains the larvae pupate, and moths emerge about three weeks later. However, the period over which pupation takes place is relatively long, generally extending from mid-October to the end of November, with the result that the earliest moths have emerged and given rise to larvae before the last diapause larvae pupate. The bulk of the larvae pupate during early November, giving rise to the main flight of moths at the end of November and early December. These moths are the source of the initial infestation under dry-land farming conditions.

In order to reduce the carry-over of *B. fusca* it is necessary to destroy all host-plants of the previous season's crop before the diapause larvae that they contain are able to pupate and give rise to moths; this need is generally recognised, but destruction is not always carried out. This is true particularly of casual African-sown crops along railway lines and in small fields near European-sown maize as well as of maize sown in and near African reserves.

Because oviposition is spread over a long period, the development of larvae and pupae of the first generation, and the flight of moths derived from them, is similarly extended. In fact, first-generation moths may be taken in the light-trap at almost any time from late January to early April, although the majority of them emerge between mid-February and mid-March (Table IV).

Large maize plants in suitable condition for larval development are available for oviposition at this time. The progeny of the earliest-formed moths of the first generation are able to complete their larval development before the maize dries out, and to pupate and emerge as moths without delay, thus constituting a short-cycle section of the second generation. Progeny of the later-formed moths constitute the normal, diapause section of the second generation. The progeny of exceptionally late-formed first-generation moths are not able to develop sufficiently to enter diapause, or, if they do so, to survive.

In the event of there being irrigated maize available in September–October for oviposition by short-cycle moths of the second generation, as, for example, in gardens or on small-holdings producing maize for consumption as a vegetable, a third generation may occur. There are many instances known of young larvae being found at this time of year on maize that has been started early under irrigation.

Observations in the field indicate that the period during which the maize stems dry out is a critical one for the borer population. There is evidence that a considerable amount of wandering from plant to plant occurs at this time and that

the population drops considerably. Presumably the larvae are more open to attack by destructive agents whilst wandering. They will bore into any object offering protection, and records of larvae from kale (Jack, 1917) and other unusual plants probably refer to such wandering larvae. It seems that in regions where weather conditions are severe during the drying out of the maize, only the larvae that find suitable resting places low in the plant survive, whereas, in Rhodesia, conditions appear to be mild enough to permit survival at all levels in the standing stem.

As already mentioned, the drying out of the maize plants coincides with the appearance of diapause larvae. By mid-June, the bulk of the larvae that will survive are in diapause.

As maize grown out of season, under irrigation, will permit continuous breeding by *B. fusca* at a time when the population bred on the main, rain-grown maize crop is in diapause, it could be an important source of infestation that would persist despite the application of routine control measures, in the form of dry-season destruction of plant residues, to the rain-grown crop. At present, the areas of irrigated maize in the Federation are very limited, but where they do occur the usual routine control measures may be ineffectual.

Summary.

The life-history and seasonal cycle of the Lepidopterous borer, *Busseola fusca* (Fuller), the most serious pest of maize in Southern Rhodesia, have been studied there.

There are two generations in the year, the majority of the full-grown larvae of the second entering diapause, in which condition the dry season is passed in the maize stem, but a proportion of the second-generation consists of short-cycle individuals that give rise to moths irregularly during the dry season.

In the field, the egg stage lasts about 7–11 days, according to the time of year. In the laboratory, there are six, very occasionally seven, larval instars in the first generation, occupying about 37 days, and the pupal stage lasts about 17 days. In the second (diapausing) generation there may be one or two additional moults without appreciable change in size, and there is considerable variation in the length of instars and in the date of entry into diapause, but by mid-June the bulk of the larvae that will survive are in diapause. The majority of diapause larvae pupate in early November, the pupal stage lasting about 23 days.

The feeding habits of the larvae are described and reference is made to other food-plants.

The length of life of the adult, in cage conditions, averages 6–7 days, but there is great variation. When provided with diluted honey, adults were not observed to feed, and absence of such food did not appear to impair egg-laying. The sex ratio was 1:1, but in catches at a light-trap the ratio of males to females was 5:1. Copulation takes place shortly after emergence, and oviposition may begin within 24 hours of emergence.

The average number of eggs laid per female in cages was 360 over an average of four days, one female laying 1,032. Several batches of eggs may be laid in one night. A single mating appears to be sufficient, but males may copulate with more than one female. Eggs laid by virgin females do not hatch.

Diapause is thought to be induced by larval feeding on drying food. Continuous rearing of non-diapause generations can be achieved by feeding the larvae on fresh, green maize. Similarly, in the field, irrigated out-of-season maize will support non-diapause generations and constitute a source of infestation that may render ineffectual the normal routine destruction of all plants of the previous dry-land farming season.

The main parasite is the Tachinid, *Sturmiopsis parasitica* (Curr.), which may destroy more than 33 per cent. of the larvae in either generation.

Acknowledgements.

I should like to thank Mr. R. Arnold and Mr. C. Moran for assistance in the laboratory and in the field. Many of the light-trap catches included were recorded by Mr. D. J. W. Rose and Mr. J. A. Whellan. Thanks are due to Mr. Walsh and Mr. Tattershill for permission to use maize lands at Gwebi Agricultural College, and to the several farmers in the Salisbury area for allowing free access to their lands.

References.

Bowden, J. (1956). New species of African stem-boring Agrotidae (Lepidoptera). —*Bull. ent. Res.* **47** pp. 415–428.

Ingram, W. R. (1958). The Lepidopterous stalk borers associated with Gramineae in Uganda.—*Bull. ent. Res.* **49** pp. 367–383.

Jack, R. W. (1917). The maize stalk borer (*Calamistis fusca*, Hmpsn.).—*Bull. Dep. Agric. S. Rhod.* no. 276, 12 pp.

Jepson, W. F. (1954). A critical review of the world literature on the Lepidopterous stalk borers of tropical Graminaceous crops.—127 pp. London, Commonw. Inst. Ent.

Mally, C. W. (1920). The maize stalk borer, *Busseola fusca*, Fuller.—*Bull. Dep. Agric. S. Afr.* no. 3, 111 pp.

du Plessis, C. & Lea, H. A. F. (1943). The maize stalk-borer *Calamistis fusca* (Hmpsn.).—*Bull. Dep. Agric. S. Afr.* no. 238, 51 pp.

Swaine, G. (1957). The maize and sorghum stalkborer, *Busseola fusca* (Fuller), in peasant agriculture in Tanganyika Territory.—*Bull. ent. Res.* **48** pp. 711–722.

© Commonwealth Agricultural Bureaux, 1959.

ACCLIMATIZATION AFFECTING THE POSITION OF THE COLD AND HEAT DEATH POINTS OF LARVAE OF *AËDES AEGYPTI* (L.).

By Kenneth Mellanby

Rothamsted Experimental Station, Harpenden, Herts.

Bar-Zeev (1957) has published data showing that larvae of the mosquito, *Aëdes aegypti* (L.), are killed in under 24 hours by exposure to a low temperature of 0·5°C., and that the thermal death point for a one-hour exposure to a high temperature is approximately 42°C. It would appear that before exposure his insects were maintained in cultures at 28°C., but no mention is made of any effects of pre-exposure temperature on the results.

I have shown (Mellanby 1939, 1940, 1954, 1958) that insects, including mosquito larvae, become acclimatized to different environmental temperatures very rapidly (usually in under 24 hours) and that this acclimatization may considerably alter their reactions at high and low temperatures. Thus the position of the chill-coma temperature, at which cold anaesthesia is produced, may be altered by several degrees in many species, and changes of a similar, though perhaps of a less striking nature, occur in the position of the thermal death point. Some insects acclimatized to warm conditions are more readily killed by cold than are cold-adapted individuals of the same species. This point was again conclusively demonstrated for the cockroach, *Blattella germanica* (L.), by Colhoun (1954).

In the experiments described here, examples of *A. aegypti* were bred and normally maintained at 30°C. Fourth-stage larvae were removed directly from this culture and exposed for various periods to a temperature of 0·5°C. An exposure of up to 7 hours had no detrimental effect; when returned to a higher temperature, either 18 or 30°C., they soon became active again, and almost all pupated and completed their life-history. On the other hand, when the exposure was extended to 17 hours, none recovered. In Table I is included the result for one batch exposed for exactly 17 hours; many other batches were in fact exposed for slightly longer or shorter periods, and gave similar results. These findings agree closely with those of Bar-Zeev (1957), who obtained a 50 per cent. mortality in 4th-stage larvae after an exposure to 0·5°C. of 14·9 hours.

Other larvae from the same culture (bred at 30°C.) were acclimatized, simply by transfer to 20, 18 and 10°C. for a period of 24 hours. Those at the two higher temperatures continued to be normally active, but those at 10°C. went into chill coma, as might have been expected for larvae previously kept at 30°C. (Mellanby, 1958). After the 24-hour period of acclimatization, the larvae were exposed to 0·5°C. for 17 hours, after which they were transferred to 18°C. The results obtained appear in Table I.

Almost all the larvae acclimatized to 20 or 18°C. survived exposure to 0·5°C. for a period of 17 hours, which was, however, always fatal to those acclimatized to 30°C. It will also be seen that little or no acclimatization took place at 10°C., at which the larvae were inactive and in chill coma. This confirms previous observations (Mellanby, 1939).

Bar-Zeev (1957) also showed that exposure to 4 and 8°C. proved lethal, but only after considerably longer periods than were fatal at 0·5°C. I made a few experiments at 5°C. All larvae from 18°C. survived 24 hours at 5°C.; only six out of a batch of 16 larvae taken directly from 30°C. survived 24 hours at 5°C.

After 65 hours at 5°C., all larvae from 30°C. were dead, while a few from 18°C. survived for a time but eventually succumbed. I have no doubt that further experiments would show considerable evidence of acclimatization influencing survival at 5°C.

TABLE I.

Result of exposure to 0·5°C. for 17 hours of 4th-stage larvae of *A. aegypti* previous acclimatized to different temperatures.

Acclimatization temperature (°C.)	30	20	18	10
Number of larvae exposed	63	122	72	108
Number surviving	0	113	66	2
Survival (%)	0	93	92	2

Earlier work on the thermal death point and acclimatization of larvae of *A. aegypti* showed that individuals acclimatized to 30°C. had a thermal death point, for a one-hour exposure, of 42°C., but that when the acclimatization temperature, was raised to 37°C., the thermal death point rose to 44°C. (Mellanby, 1954).

We see therefore that the effects of extreme temperatures, at both the hot and cold ends of the scale, may be substantially modified by a brief period of acclimatization. This process is not only rapid; it is completely reversible. The physiological mechanism behind this acclimatization is still a mystery, but then so is the cause of death within 17 hours at 0·5°C. and for that matter after one hour at 42 or 44°C.

In these and in many previous experiments (*e.g.*, Mellanby, 1932) I have found it convenient to measure the thermal death point, that is, the temperature at which death occurs when insects are exposed for a particular period (often one or 24 hours). Recently many workers, including Bar-Zeev (1957) have preferred to use the T 50, that is, to determine the time required for exactly 50 per cent. of the insects exposed to be killed. This method has proved itself invaluable for tests of insecticides, and I agree that ideally it is the technique that should be used in studying lethal effects of temperature, but it is much more time-consuming than simple thermal death point determinations. Unless the experimenter has unlimited time and material at his disposal, I would suggest that, provided care is taken to use reasonably uniform batches of insects, very nearly as much information can be obtained in a much shorter time by the older, simpler, technique. So often, particularly with exposures of one hour, there is less than 1°C. between the temperature giving 100 per cent. mortality and that at which all individuals survive, that little is gained by intensive studies of varying exposures to a great number of temperatures.

Summary.

In experiments with *Aëdes aegypti* (L.), fourth-stage larvae bred at 30°C. survived exposure to 0·5°C. for 7 hours, but none recovered after exposure for 17 hours, although nearly all those from the same culture that had been acclimatized for one hour to 18 or 20°C. did so. No such effect followed acclimatization at 10°C., at which larvae are in chill coma. Larvae acclimatized at 18°C. survived exposure to 5°C. for longer than did those from 30°C. Earlier work showed that the thermal death point, for a one-hour exposure, was 42°C. for larvae acclimatized at 30°C. but rose to 44°C. for larvae acclimatized to 37°C. It is concluded that the effects of high or low extremes of temperature may be substantially modified by a brief period of acclimatization at a less extreme temperature.

References.

BAR-ZEEV, M. (1957). The effect of extreme temperatures on different stages of *Aëdes aegypti* (L.).—*Bull. ent. Res.* **48** pp. 593–599.

COLHOUN, E. H. (1954). Temperature acclimatization in insects.—*Nature, Lond.* **173** p. 582.

MELLANBY, K. (1932). The influence of atmospheric humidity on the thermal death point of a number of insects.—*J. exp. Biol.* **9** pp. 222–231.

MELLANBY, K. (1939). Low temperature and insect activity.—*Proc. roy. Soc.* (B) **127** pp. 473–487.

MELLANBY, K. (1940). The activity of certain Arctic insects at low temperatures. —*J. Anim. Ecol.* **9** pp. 296–301.

MELLANBY, K. (1954). Acclimatization and the thermal death point in insects.— *Nature, Lond.* **173** pp. 582–583.

MELLANBY, K. (1958). The alarm reaction of mosquito larvae.—*Ent. exp. appl.* **1** pp. 153–160.

© Commonwealth Agricultural Bureaux, 1959.

GENERAL INDEX.

A.

abnormalis, Aëdes (*Aëdimorphus*).
abnormis, Leptomastidea.
abrupta, Crematogaster (*Rhachiocrema*).
acanthosceles, Coccophagus.
Acerophagus pallidus, **430.**
aconitus, Anopheles.
Acrocoelia (see *Crematogaster*).
Acropyga moluccana papuana, **133.**
adansonii, Apis mellifera.
adersi, Aëdes (*Diceromyia*).
adersianus, Culex (*Neoculex*).
adonidum, Pseudococcus.
adusta, Povilla.
Aëdes, biting habits and medical importance of subgenera *Aëdimorphus*, *Banksinella* and *Dunnius* of, in East Africa, **759–779.**
Aëdes abnormalis, **193, 763, 764, 765, 772, 773.**
Aëdes abnormalis kabwachensis, **765.**
Aëdes adersi, **193, 196, 199.**
Aëdes aegypti, in Kenya, **191–208, 687–696;** in Nigeria, **681–686;** in Uganda, **227–235;** biting cycle of, **191–208, 227–235, 687–696;** breeding habits of, **681–686;** effect of acclimatization on cold and heat death points of, **821–823;** effects of insecticides on, **156, 682, 683, 684, 685.**
Aëdes aegypti aegypti, **681, 689.**
Aëdes aegypti formosus, in East Africa, **227–235, 689.**
Aëdes aegypti queenslandensis, **689.**
Aëdes africanus, **773.**
Aëdes albicosta, **192, 196, 204, 205, 206, 775.**
Aëdes albocephalus, **192, 196, 206, 764.**
Aëdes albomarginatus, **761, 771, 773.**
Aëdes albothorax, **205, 761, 771.**
Aëdes apicoannulatus, **761, 773.**
Aëdes apicoargenteus, **228.**
Aëdes argenteopunctatus, **193, 761, 762, 772, 773.**
Aëdes calceatus, **193, 196.**
Aëdes capensis, **761, 762.**
Aëdes circumluteolus, **763, 768, 769, 770, 771, 772, 773, 774, 775.**
Aëdes congolensis, **765.**
Aëdes cumminsi, **196, 763, 766, 767, 772, 773.**
Aëdes cumminsi mediopunctatus, **193, 196.**
Aëdes deboeri demeilloni, **773.**
Aëdes dendrophilus, **773.**
Aëdes dentatus, **766.**
Aëdes domesticus, **761, 762, 763.**
Aëdes ellinorae, **193.**
Aëdes fryeri, **199.**
Aëdes fulgens, **193, 196.**
Aëdes furcifer, **199.**
Aëdes haworthi, **193, 196, 199, 761, 762, 773.**
Aëdes heischi, **193, 196.**
Aëdes ingrami, **774.**
Aëdes lamborni, **760, 773.**
Aëdes leptolabis, **761, 762, 763.**
Aëdes lineatopennis, **205, 768, 775.**
Aëdes longipalpis, **774.**
Aëdes metallicus, **192, 194, 196, 198, 200, 202, 204.**
Aëdes mucidus, **196.**
Aëdes mutilus, **761, 762, 772, 773.**
Aëdes natronius, **761, 767, 768, 773, 774.**
Aëdes ochraceus, **760.**
Aëdes palpalis, **763, 769, 770, 773, 774.**
Aëdes pembaensis, **192, 194, 195, 196, 197, 198, 200, 201, 204, 205, 689.**
Aëdes phyllolabis, **764.**
Aëdes punctocostalis, **771, 773.**
Aëdes scatophagoides, **193, 196, 199.**
Aëdes semlikiensis, **765.**
Aëdes simpsoni, **192, 196, 197, 198, 200, 202, 203, 204, 689.**
Aëdes simulans, **761, 762, 773.**
Aëdes smithburni, **764.**
Aëdes stokesi, **761, 762, 773.**
Aëdes taeniarostris, **771, 773, 774.**
Aëdes tarsalis, **193, 196, 763, 764, 765, 773.**
Aëdes taylori, **199.**
Aëdes tricholabis, **193, 196.**
Aëdes tricholabis bwamba, **765.**
Aëdes vexans, **767.**
Aëdes vittatus, **193, 196.**
Aëdes wigglesworthi, **765.**
Aëdimorphus (see *Aëdes*).
Aëdomyia furfurea, **196.**
aegypti, Aëdes.

aequinoctiale, *Gibbium*.
affine, *Mezium*.
affinis, *Polyrhachis*.
africana, *Mansonia* (*Mansonioides*, *Taeniorhynchus*).
africanus, *Aëdes*; *Neanastatus*.
Agathis gibbosa, **426.**
agilis, *Linnaemyia*.
agnatus, *Ptinus*.
Agrostis stolonifera, Dipterous larvae injuring, **58.**
Agrostis tenuis, Dipterous larvae injuring, **53, 54, 55, 56, 58.**
Aircraft, insecticides applied from, against *Aëdes aegypti*, **682, 683, 684.**
albicosta, *Aëdes* (*Banksinella*).
albipes, *Technomyrmex*.
albiseta, *Oscinella*.
albiventris, *Culex* (*Neoculex*).
alboabdominalis, *Uranotaenia*.
albocephalus, *Aëdes* (*Aëdimorphus*).
albomarginatus, *Aëdes* (*Dunnius*).
albothorax, *Aëdes*.
Aldrin, against Diptera, **72, 781–793, 795–807**; against Hemiptera, **17, 18, 19, 723, 724, 726, 732.**
Aleurodothrips fasciapennis, **425.**
aleyrodiformis, *Semidalis*.
Allotropa citri, **430.**
Alopecurus pratensis, Dipterous larvae injuring, **58.**
Amblypelta, relation of ants to species of, causing nutfall of coconut in Solomon Is., **97-133, 523–558, 559–566.**
Amblypelta cocophaga, **119, 120, 121, 122, 123, 124, 125, 523, 552, 559–566.**
Amblypelta cocophaga cocophaga, **119, 123, 561, 564.**
Amblypelta cocophaga malaitensis, **119, 123, 561.**
Amblypelta costalis, **119, 120, 121.**
Amblypelta costalis costalis, **119.**
Amblypelta costalis rennellensis, **119.**
Amblypelta cristobalensis, **119, 120, 121, 122, 125.**
Amblypelta gallegonis, **119, 120, 121.**
Amblypelta gallegonis bougainvillensis, **119.**
Amblypelta gallegonis gallegonis, **119.**
americanum, *Mezium*.
Amphorophora rubi (on raspberry), new strains of, in England, **81–87**; possible distinct strain of, in Holland, **86.**
Anabrolepis zetterstedtii, **427.**
anacardii, *Helopeltis*.
Anacardium occidentale (see Cashew).
Anagasta kühniella, **712.**
Anagrus pseudococci, **430.**
Anagyrus fusciventris, **430.**
Anarhopus sydneyensis, **430.**
Anastatus axiagasti, **563, 564.**
Anastatus axiagasti rufithorax, **563.**
anceps, *Iridomyrmex*.
Ancylostomia stercorea, bionomics and parasites of, on pigeon pea in Trinidad, **737–757**; distribution of, **737.**
Aneristus, **431.**
Aneristus ceroplastae, **431, 432.**
angelicus, *Pseudaphycus*.
Angitia blackburni, **426.**
Angitia compressa, **426.**
angolensis, *Chilocorus*.
angustifrons, *Aphycus* (*Metaphycus*).
Anicetus, **431.**
Anisopteromalus, **666.**
annae, *Polyrhachis* (*Hedomyrma*).
annularis, *Anopheles*.
annulata, *Myopsocnema*.
annulatum, *Eiphosoma*.
annulioris, *Culex*.
Anochetus punctiventris oceanicus, **132.**
Anolis spp., relation of, to biological control of Coccids in Bermuda, **424, 430, 432, 433.**
Anomala exitialis, in tobacco fields in S. Rhodesia, **89–96, 259–263**; fungous diseases of, **89–96.**
Anomala (*Phyllopertha*) *horticola*, biology and ecology of, in Britain, **39–52, 467–486.**
Anopheles aconitus, bionomics of, in Java, **647–660**; and malaria, **647, 658, 659.**
Anopheles annularis, bionomics of, in Java, **647–660.**
Anopheles barbirostris, bionomics of, in Java, **647–660.**
Anopheles coustani, **193, 196.**
Anopheles coustani tenebrosus, **193, 196, 688.**
Anopheles coustani ziemanni, **193, 196, 228.**
Anopheles funestus, **193, 194, 195, 196, 200, 206, 688.**
Anopheles gambiae, **193, 194, 196, 199, 200, 206, 688.**
Anopheles kochi, bionomics of, in Java, **647–660.**
Anopheles maculatus, bionomics of, in Java, **647–660**; and malaria, **647, 658, 659.**
Anopheles maculipalpis, **199.**
Anopheles paludis, **193, 196.**
Anopheles pharoensis, **193, 196.**
Anopheles rhodesiensis, **688.**
Anopheles squamosus, **193, 196.**
Anopheles subpictus malayensis, bionomics of, in Java, **647–660.**

Anopheles tessellatus, bionomics of, in Java, **647–660.**
Anopheles vagus, bionomics of, in Java, **647–660.**
Anoplolepis custodiens, relation of, to *Pseudotheraptus wayi* on coconut in Zanzibar, **135–149.**
Anoplolepis longipes, relation of, to Coreid pests of coconut in Solomon Is. and Zanzibar, **97–133, 135–149, 151–164, 523–558, 565;** effects of insecticides on, **151–164.**
antennatus, *Culex*.
Anthoxanthum odoratum, Dipterous larvae injuring, **54, 55, 56, 58, 61.**
Antigua, *Ancylostomia stercorea* in, **737.**
antiqua, *Delia*.
Apanteles, **502, 503.**
Apanteles dignus, **426.**
Apanteles etiellae, **754.**
Apanteles etiellae isolatus, bionomics of, parasitising *Ancylostomia stercorea* in Trinidad, **738, 739–741, 743;** parasites of, **754;** rearing of, **741;** introduced into Mauritius, **755.**
Apanteles ultor, **501.**
Aphis fabae, used in tests of systemic action of insecticides, **25–38.**
Aphomia gularis, in imported shelled walnuts in Britain, **711–716.**
Aphycus, **432.**
Aphycus angustifrons, **431.**
Aphycus flavus, **431.**
Aphycus luteolus, **431.**
Aphycus stanleyi, **431.**
Aphytis, **427, 428.**
Aphytis chrysomphali, **427.**
Aphytis diaspidis, **424.**
Aphytis fuscipennis, **425.**
Aphytis lingnanensis, **424.**
Aphytis mytilaspidis, **425, 427.**
Aphytis proclia, **424.**
apicoannulatus, *Aëdes*.
apicoargenteus, *Aëdes* (*Stegomyia*).
Apis mellifera adansonii, **160.**
Arachis hypogaea (see Groundnuts).
argenteopunctatus, *Aëdes* (*Aëdimorphus*).
Argentochernes (see *Parachernes*).
Argyroploce leucotreta, **491, 494.**
armigera, *Heliothis*.
Arrenoclavus koehleri, **426.**
Arrhenatherum elatius, Dipterous larvae injuring, **54, 55, 58.**
Aschersonia, **440.**
Ascogaster cava, **501.**
Asphondylia sesami, on *Sesamum orientale* in Nigeria, **665;** parasites of, **666.**
Aspidiotiphagus citrinus, **424, 425.**
Aspidiotiphagus lounsburyi, **424, 428.**
Asterolecanium bambusae, **428.**
Atherurus africanus, **643.**
atoma, *Paratrechina minutula*.
Atomised Sprays, effect of droplet size on deposition of, on dead houseflies, **327–332.**
aurantii, *Prospaltella*; *Toxoptera*.
austeni, *Glossina*.
axiagasti, *Anastatus*.
Axiagastus cambelli, **565.**
Azotus, **427.**
Azya luteipes, **427, 432.**
Azya trinitatis, **427.**

B.

bambusae, *Asterolecanium*.
Banana Scab Moth (see *Nacoleia octasema*).
Banksinella (see *Aëdes*).
barberi, *Sympherobius*.
barbirostris, *Anopheles*.
Barley, *Oscinella frit* on, **61.**
Barringtonia, *Coccus hesperidum* on, **542.**
Beans, seed treatments of, against *Melanagromyza phaseoli* in Tanganyika, **781–793;** *Heliothis armigera* on, in Uganda, **488, 493, 498.**
Beans, Broad, used in tests of systemic action of insecticides, **25–38.**
Beauveria bassiana, **91, 92.**
bedoti, *Camponotus reticulatus*.
belli, *Camponotus*; *Pheidolacanthinus*.
bellus, *Microdon*.
Bemisia tabaci, factors affecting infestation of cotton by, in Sudan, **569, 577, 579, 586, 587, 591.**
bennetti, *Phanerotoma*.
Benniseed Gall Midge (see *Asphondylia sesami*).
bergrothi, *Helopeltis*.
berlesei, *Prospaltella*.
Bermuda, biological control of insect pests in, **423–436.**
Bermuda Cedar (see *Juniperus bermudiana*).
bhavanae, *Ceratopheidole*.
BHC, against Diptera, **63–80, 781–793;** against locusts, **380;** against Mirids, **13–23, 174–180;** against other Hemiptera, **151, 152, 161, 717–735;** as lindane, **151, 152, 161.**
bicinctus, *Ptinus*.
biclavis, *Howardia*.
bifasciata, *Comperiella*.
binaevatus, *Scymnus*.
biplaga, *Earias*.
bipustulatus, *Chilocorus*.
bisbinotatus, *Exochomus*.

Bis(dimethylamino)fluorophosphine Oxide (see Dimefox).
Bis(dimethylamino)phosphonous Anhydride (see Schradan).
bivulnerus, Chilocorus (see *C. stigma*).
Blackberry, experiments with *Amphorophora rubi* and, **83, 86.**
blackburni, Angitia.
Blattisocius tineivorus, **303.**
bogoriensis, Coccophagus.
boieldieui, Gibbium.
Bothriomyrmex, **133.**
Bothriomyrmex flavus, **133.**
Bothriomyrmex pusillus, **107, 116, 117, 118, 133, 550, 551, 552, 553, 554.**
bougainvillensis, Amblypelta gallegonis.
bourbonica, Paratrechina.
Brachymeria, **501.**
Brachytrupes membranaceus, **91.**
Bracon, **754.**
Bracon cajani, bionomics of, parasitising *Ancylostomia stercorea* in Trinidad, **738, 749, 750**; establishment of, in Mauritius, **755.**
Bracon gelechiae, **426.**
Bracon hebetor, **712.**
Bracon thurberiphagae, **754**; bionomics of, parasitising *Ancylostomia stercorea* in Trinidad, **738, 747–749**; attempted rearing of, **749**; introduced into Mauritius, **755.**
brasiliensis, Sphaericus.
brassicae, Brevicoryne; *Pieris.*
brevibucca, Chironomus.
Brevicoryne brassicae, used in tests of systemic action of insecticides, **25–38.**
brevipalpis, Toxorhynchites.
Britain, pests of grasses and cereals in, **39–52, 53–62, 467–486**; *Delia antiqua* on onion in, **795–807**; new strains of *Amphorophora* on raspberry in, **81–87**; *Culicoides impunctatus* in, **63–80**; pests of stored products in, **287–326, 407–422, 711–716.**
Brontispa, **113.**
browni, Pristhesancus.
brucei, Trypanosoma.
Bruchoptinus (see *Ptinus*).
Buffalo, Dwarf Forest (see *Syncerus nanus*).
Bufo marinus, **423.**
Bunyamwera Virus, **773, 774, 775.**
Bushbuck (see *Tragelaphus scriptus*).
Busseola fusca, bionomics of, on maize in S. Rhodesia, **809–819.**
Byssodon (see *Simulium*).

C.

Cabbage, used in tests of systemic action of insecticides, **25–38.**
Cacao, pests and swollen-shoot virus of, in Ghana, **11–12, 13–23, 209**; trunk implantation of, with dimefox, **209–225**; injured by 10 DRDK, **157.**
cacti, Chilocorus.
Cages, for rearing *Stomoxys*, **165, 166.**
cajani, Bracon.
Cajanus cajan (Pigeon Pea), Pyralids on, in Mauritius, **737, 754**; *Ancylostomia stercorea* on, in Trinidad, **737.**
Calandra oryzae, bionomics of small strain of, on stored rice in Sierra Leone, **697–702.**
Calandra sasakii, **697.**
calceatus, Aëdes (*Stegomyia*).
calcitrans, Stomoxys.
californicus, Ptinus (*Gynopterus*).
Caliothrips, **577, 588, 591.**
callidum, Simulium (*Psilopelmia*).
Callosobruchus maculatus, bionomics of abnormal form of, on cowpea in Nigeria, **671–680.**
Calomel, against *Delia antiqua*, **795–807.**
Calonectria rigidiuscula, **13.**
Calpodes ethlius, biological control of, in Bermuda, **429.**
cambelli, Axiagastus.
campestris, Lyctocoris.
Camponotus, **133, 152, 155.**
Camponotus belli, **116.**
Camponotus chloroticus, **116.**
Camponotus irritans, **118, 542.**
Camponotus irritans samoaensis, **107, 116, 117, 133, 552.**
Camponotus maculatus, **156.**
Camponotus reticulatus bedoti, **107, 116, 117, 118, 133, 552.**
Camponotus rufoglaucus, **156.**
Camponotus sanctae crucis, **116.**
Camponotus vividus, **156.**
Campoplex phthorimaeae, **426.**
Canada, *Ancylostomia stercorea* in, **737.**
Canna Leaf Roller (see *Calpodes ethlius*).
capensis, Aëdes (*Aëdimorphus*); *Netelia.*
capitata, Ceratitis.
Capnodium, **440.**
Capsicum, injured by 10 DRDK, **157.**
cardinalis, Rodolia.
Cardiochiles trimaculatus, **501, 502, 503.**
Cardiocondyla nuda, **132, 555.**
Carpophilus, **173.**
Carpophilus obsoletus, **237.**
Carulaspis, **427.**
Carulaspis minima, biological control of, in Bermuda, **423, 426–429.**
Cashew, *Helopeltis* spp. on, in Tanganyika, **171–181.**
Cassava (see *Manihot esculenta*).
castanea, Pentilia.
castaneum, Tribolium.

Cattle, relation of Anophelines to, **647–660**; *Glossina* spp. and trypanosomiasis of, **595–615, 637, 638, 639, 642, 644**; *Stomoxys* possibly transmitting trypanosomiasis of, **165.**
cautella, *Ephestia.*
cava, *Ascogaster.*
Cedar, Bermuda (see *Juniperus bermudiana*).
cephalonica, *Corcyra.*
Cephalonomia gallicola, **303.**
Cephalophus maxwellii, **609, 625.**
Cephalophus rufilatus, **609, 625.**
Cephaloscymnus occidentalis, **427, 428.**
Ceraphron, **501.**
Ceratitis capitata, biological control of, in Bermuda, **424.**
Ceratopheidole bhavanae, relation of *Eriochiton theae* on tea to, in India, **438, 439, 440.**
Cercopithecus aethiops tantalus, **609.**
Cercopithecus ascanius schmidti, **773.**
Cercopithecus mona, **609.**
Cereals, pests of, in Britain, **53–62.** (See Maize, Rice, etc.)
ceroplastae, *Ameristus.*
Ceroplastes, **177.**
Cetema, injuring wheat and grasses in England, **54, 55, 56, 58, 59, 61.**
Cetema elongata, **55.**
Cetema neglecta, **55.**
Ceylon, *Scotinophara lurida* on rice in, **717–735.**
Ceylon Oak (see *Schleichera trijuga*).
chalazopa, *Ptochoryctis.*
chalybeus, *Orcus.*
Charops, **501, 502, 503.**
Charyomyrma (see *Polyrhachis*).
Cheiloneurus pulvinariae, **431.**
Chelonus phthorimaeae, **426.**
Cheyletus eruditus, **303.**
Chillie (see *Capsicum*).
Chilocorus angolensis, **431.**
Chilocorus bipustulatus, **424, 427.**
Chilocorus bivulnerus (see *C. stigma*).
Chilocorus cacti, **425, 427, 428, 433, 434.**
Chilocorus distigma, **427.**
Chilocorus nigritus, **427.**
Chilocorus stigma, **427.**
Chironomus brevibucca, lunar rhythm of emergence in, **1–8.**
Chlordane, against *Culicoides impunctatus*, **72, 76, 77, 79**; against Mirids, **17, 18**; against *Scotinophara lurida*, **722, 723, 732.**
Chlorops pumilionis, **60.**
chloroticus, *Camponotus.*
Chlorthion, against *Scotinophara lurida*, **717, 718, 719, 723, 725, 726, 732.**
Chnoodes, **427.**
Chnoodes cinctipennis, **427.**
chrysomphali, *Aphytis.*
Chrysopa, **272, 444.**
chrysosoma, *Mansonia* (*Taeniorhynchus*).
cinctipennis, *Chnoodes.*
cinereus, *Culex* (*Culiciomyia*).
circumluteolus, *Aëdes* (*Banksinella*).
citri, *Allotropa*; *Planococcus.*
citricola, *Coccidophilus.*
citrinus, *Aspidiotiphagus.*
Citrus, pests of, in Bermuda, **423–436.**
clavatus, *Tyndarichus.*
clavicornis, *Nausibius.*
clavipes, *Ptinus.*
Cleis picta, **428.**
coarctata, *Leptohylemyia.*
coarcticollis, *Ptinus* (*Pseudoptinus*).
Coccidophilus citricola, **425.**
Coccinella novemnotata, **428.**
coccivora, *Scymnus.*
Coccophagus acanthosceles, **440.**
Coccophagus bogoriensis, **431.**
Coccophagus hawaiiensis, **431.**
Coccophagus lecanii (see *C. lycimnia*).
Coccophagus lycimnia, **431.**
Coccophagus mexicanus, **432.**
Coccus discrepans, **438, 440.**
Coccus elongatus, **542.**
Coccus hesperidum, in Bermuda, **428, 431**; in India, **437–448**; in Solomon Is., **538, 542**; on *Barringtonia*, **542**; on *Citrus*, **431, 538**; on tea, **437–448**; relation of ants to, **437–448, 538, 542**; biological control of, **428, 431.**
Coccus mangiferae, **538, 542.**
Coccus viridis, **542**; biological control of, in Bermuda, **428, 431.**
Coconut, insects associated with immature nutfall of, in Solomon Is., **97–133, 523–558, 559–566**; *Pseudotheraptus wayi* and associated insects on, in Zanzibar, **135–149, 151–164.**
cocophaga, *Amblypelta.*
Cocos nucifera (see Coconut).
Codiacum variegatum, *Planococcus citri* on, in Bermuda, **430.**
coeruleus, *Curinus.*
coffeae, *Oligonychus*; *Saissetia.*
Colobopsis (see *Camponotus*).
combinata, *Geomyza.*
communis, *Enicospilus.*
Comperiella bifasciata, **424.**
compressa, *Angitia.*
Comstockiella sabalis, biological control of, in Bermuda, **425, 428, 434.**
confluens, *Pentilia.*
congolense, *Trypanosoma.*
congolensis (*Aëdimorphus*), *Aëdes.*

Conioscinella spp., injuring grasses in England, **54, 58.**
consimilis, Culex annulioris.
Copidosoma, **667.**
Coquillettidia (see *Mansonia*).
Corchorus capsularis (see Jute).
Corcyra cephalonica, **744.**
Cordyceps, **91.**
Cordyceps myrmecophila, **91.**
corticivora, Deloryctis.
costalis, Amblypelta.
Cotton, pests of, in Sudan, **567–594;** Lepidoptera on, in Uganda, **487–506;** effect of DDT sprays on yield of, **567–594.**
coustani, Anopheles.
Cowpea, *Callosobruchus maculatus* on, in Nigeria, **671–680.**
Crematogaster, **132, 152, 438, 439, 444, 445.**
Crematogaster abrupta, **132.**
Crematogaster dohrni, relation of, to Coccids on tea in India, **437–448.**
Crematogaster obnigra, **132.**
Crematogaster scita, **132.**
cristobalensis, Amblypelta.
Croton (see *Codiacum variegatum*).
crucis, Camponotus sanctae.
Cryptochetum iceryae, **423, 424, 434.**
Cryptognatha, **425.**
Cryptognatha nodiceps, **425, 427.**
Cryptognatha simillima, **425.**
Cryptognatha tumidiventris, **427.**
Cryptolaemus montrouzieri, **425, 429, 430, 432.**
Cryptophagus subfumatus, **712, 713, 714.**
Cryptus ptinivorus, **303.**
Cucumber, injured by 10 DRDK, **157.**
Culex, **689, 773.**
Culex adersianus, **193.**
Culex albiventris, **193.**
Culex annulioris, **193, 196.**
Culex annulioris consimilis, **228.**
Culex antennatus, **193, 196, 200, 689.**
Culex cinereus, **193, 194, 196.**
Culex decens, **193, 194, 196, 199, 200.**
Culex duttoni, **192, 194, 198, 200, 201, 202.**
Culex furlongi, **193, 196.**
Culex grahami, **193, 196.**
Culex guiarti, **193.**
Culex horridus, **191, 192, 194, 196.**
Culex inconspicuosus, **196.**
Culex insignis, **193.**
Culex invidiosus, **193, 196.**
Culex moucheti, **772.**
Culex nebulosus, **192, 196, 201.**
Culex ornatothoracis, **193.**
Culex perfuscus, **193, 196.**
Culex pipiens fatigans, **156;** in Kenya, **191–208, 689;** biting cycle of, **191–208.**
Culex poicilipes, **193, 196.**
Culex semibrunneus, **193.**
Culex simpsoni, **193, 689.**
Culex sitiens, **193, 194, 196, 199, 200, 689.**
Culex tigripes, **192, 202.**
Culex trifoliatus, **193.**
Culex tritaeniorhynchus, **193, 196, 689.**
Culex univittatus, **193, 196, 689.**
Culex weschei, **196.**
Culex weschei gediensis, **193, 196.**
Culex wigglesworthi, **193.**
Culiciomyia (see *Culex*).
Culicoides impunctatus, larvicides against, in Scotland, **63–80.**
cumminsi, Aëdes.
cupreoviridis, Earias.
Curinus coeruleus, **427.**
curvimaculata, Neochelonella.
custodiens, Anoplolepis.
Cybocephalus, **425, 427, 428.**
Cybocephalus rufifrons, **427.**
Cycas revoluta, Pseudococcus adonidum on, **430.**
Cycloneda sanguinea, **427, 428.**
Cyphoderes (see *Ptinus*).
cyptopus, Hodgesia.
Cyrtomyrma (see *Polyrhachis*).

D.

Dactylis glomerata, Dipterous larvae injuring, **53, 54, 55, 58.**
dactylopii, Leptomastix.
damnosum, Simulium.
DDT, against Diptera, **63–80, 682, 683, 684, 782, 783, 784, 795–807;** against Mirids, **13–23, 174, 176, 177, 180;** against other Hemiptera, **151–164, 567–594, 717, 718, 719, 720, 722, 732;** effect of, on yield of cotton, **567–594.**
deboeri, Aëdes (*Stegomyia*).
decens, Culex.
Delia antiqua, seed treatments against, on onion in Britain, **795–807.**
Delia florilega, **60.**
Deloryctis corticivora, on rubber and *Schleichera trijuga* in Malaya and Java, **9, 10.**
demeilloni, Aëdes (*Stegomyia*) *deboeri.*
dendrophilus, Aëdes (*Stegomyia*).
dentatus, Aëdes (*Aëdimorphus*).
Dermestes lardarius, **712.**
destructor, Glycyphagus.
detorquens, Technomyrmex.
diaspidicola, Prospaltella.
diaspidis, Aphytis.

Diazinon, against *Melanagromyza phaseoli*, **784, 785**; against *Scotinophara lurida*, **717–735.**
Diceromyia (see *Aëdes*).
Dieldrex, **382.**
Dieldrin, **161**; against Diptera, **72, 76, 79, 682, 683, 684, 781–793, 795–807**; against Hemiptera, **17, 18, 19, 717–735**; against locusts, **371–386**; toxicity of, to sheep and goats, **384.**
dignus, *Apanteles.*
Dimachus discolor, **303.**
Dimefox, trunk implantation of cacao with, against mealybugs, **209–225.**
O,O-Dimethyl S-(4-Oxo-benzotriazino-3-methyl) Phosphorodithioate (see Guthion).
Dimethyl 2,2,2-Trichloro-1-hydroxyethylphosphonate (see Dipterex).
diminuta, *Leptogenys* (*Lobopelta*).
Diocalandra frumenti, **160.**
Diplomorium, **132.**
Dipterex, against *Melanagromyza phaseoli*, **784, 785**; against *Scotinophara lurida*, **717–735.**
discolor, *Dimachus.*
discrepans, *Coccus.*
Distantiella theobroma, insecticides against, on cacao in Ghana, **13–23**; method of rearing, **11–12.**
distigma, *Chilocorus.*
distinguendus, *Lariophagus.*
diversipes, *Lioscymnus.*
dohrni, *Crematogaster.*
domestica, *Musca.*
domesticus, *Aëdes* (*Aëdimorphus*); *Glycyphagus.*
Dominica, *Ancylostomia stercorea* in, **737**; parasite of *A. stercorea* in, **750.**
douei, *Procula.*
10 DRDK, **151, 153, 154, 155, 157, 158, 160, 161, 163.**
Drosophila, **173.**
dugesi, *Simulium* (*Psilopelmia*).
Duiker, Crowned (see *Sylvicapra grimmia*).
Duiker, Maxwell's (see *Cephalophus maxwellii*).
Duiker, Red-flanked (see *Cephalophus rufilatus*).
Dunnius (see *Aëdes*).
Dutrex 3, **363, 379.**
Dutrex 55, **379.**
Dutrex 130, **379.**
duttoni, *Culex.*
Dysdercus fasciatus, effects of temperature on growth and reproduction of, **387–405.**

E.

Earias, **491, 494, 495, 503.**
Earias biplaga, **491.**
Earias cupreoviridis, **491.**
Earias insulana, **491, 577, 580, 581.**
earlei, *Simulium* (*Hemicnetha*).
Egius platycephalus, **427.**
Egretta, **732.**
Eiphosoma annulatum, **754**; bionomics of, parasitising *Ancylostomia stercorea* in Trinidad, **738, 744–747**; attempted rearing of, **746**; establishment of, in Mauritius, **755.**
Ekatin, against *Scotinophara lurida*, **727, 728, 729, 730, 731, 733.**
Elachertus meridionalis, **429.**
elatior, *Technomyrmex modiglianii.*
Elephant, African Savannah (see *Loxodonta africana*).
ellingseni, *Paratemnus.*
ellinorae, *Aëdes* (*Banksinella*).
elongata, *Cetema.*
elongatus, *Coccus.*
Empoasca lybica, effect of DDT sprays on infestation of cotton by, in Sudan, **567–594.**
Enarmonia, **712, 713, 714.**
Encarsia portoricensis, **425.**
Endrin, **161**; against *Melanagromyza phaseoli*, **781–793**; against *Scotinophara lurida*, **717–735.**
Enicmus minutus, **712.**
Enicospilus, **502, 503.**
Enicospilus communis, **501.**
entomophagus, *Thyreophagus.*
Ephestia cautella, **743, 744.**
Epipremnum pinnatum, *Coccus mangiferae* on, **542.**
epius, *Spalgis.*
Eretmapodites, **773.**
Eretmapodites grahami, **772.**
Eretmapodites quinquevittatus, **192, 196, 206.**
Eretmapodites silvestris, **193, 196.**
Eretmapodites subsimplicipes, **192, 196, 206.**
Eriochiton theae, relation of ants to, on tea in India, **437–448.**
Eritrea, *Schistocerca gregaria* in, **378, 379, 381.**
eruditus, *Cheyletus.*
Erythrocebus patas, **609.**
Ethiopia, *Schistocerca gregaria* in, **374, 382–383.**
ethlius, *Calpodes.*
Etiella zinckenella, **737, 754.**
etiellae, *Apanteles.*
Euglandia rosea, **432.**
Eupelmus, **754.**

Euponera stigma, **132.**
Euponera stigma quadridentata, **132.**
Eurytoma, **501, 666, 754.**
exarator, *Spathius.*
exiguus, *Pharoscymnus.*
exitialis, *Anomala.*
Exochomus bisbinotatus, **427.**
Exochomus jamaicensis, **427.**
Exochomus quadripustulatus, **427.**
Exochomus ritchiei, **427.**
exulans, *Ptinus* (*Gynopterus*).

F.

fabae, *Aphis.*
familiare, *Theridion.*
fasciapennis, *Aleurodothrips.*
fasciatus, *Dysdercus.*
fatigans, *Culex pipiens.*
femorata, *Ficalbia* (*Mimomyia*).
Ferrisiana virgata, **209.**
Festuca spp., Dipterous larvae injuring, **58, 59.**
Ficalbia femorata, **228.**
Ficalbia mimomyiaformis, **193.**
Ficalbia plumosa, **193, 196.**
Ficalbia splendens, **193.**
Ficus, *Pulvinaria psidii* on, in Bermuda, **431.**
Ficus septica, Coccids on, in Solomon Is., **542.**
Finlaya (see *Aëdes*).
flavus, *Aphycus* (*Metaphycus*); *Bothriomyrmex.*
floricola, *Monomorium.*
floridanus, *Horismenus.*
florilega, *Delia.*
florum, *Opomyza.*
Fluoroacetamide, tests of systemic and insecticidal action of, **25–38.**
foreli, *Plagiolepis.*
formicarii, *Saissetia.*
formosus, *Aëdes aegypti.*
France, pests of shelled walnuts imported into Britain from, **711–716.**
fraterculus, *Monomorium.*
frit, *Oscinella.*
froggatti, *Rhytidoponera.*
frontella, *Conioscinella.*
frumenti, *Diocalandra.*
fryeri, *Aëdes.*
fulakora, *Polyrhachis* (*Cyrtomyrma*) *rastellata.*
fulgens, *Aëdes* (*Finlaya*).
fumipennis, *Pristomerus.*
funestus, *Anopheles* (*Myzomyia*).
fur, *Ptinus.*
furcifer, *Aëdes.*
furfurea, *Aëdomyia.*
furlongi, *Culex* (*Culiciomyia*).
fusca, *Busseola*; *Glossina.*
fuscescens, *Pheidolacanthinus.*
fuscipennis, *Aphytis.*
fuscipes, *Glossina palpalis.*
fusciventris, *Anagyrus.*
fuscopennata, *Mansonia* (*Coquillettidia*).

G.

gallegonis, *Amblypelta.*
gallicola, *Cephalonomia.*
gambiae, *Anopheles* (*Myzomyia*).
gambiense, *Trypanosoma.*
gandolphei, *Ptinus.*
Garden Chafer (see *Anomala horticola*).
gediensis, *Culex weschei.*
gelechiae, *Bracon.*
genitalis, *Phorbia.*
Geomyza, **61.**
Geomyza combinata, injuring grasses in England, **54, 56, 58, 61.**
Geomyza tripunctata, injuring grasses in England, **54, 58.**
germinationis, *Opomyza.*
Ghana, pests and swollen-shoot of cacao in, **11–12, 13–23, 209–225**; *Glossina* spp. and *Trypanosoma vivax* in, **183–189.**
Gibbium, **287.**
Gibbium aequinoctiale, **287, 290, 294.**
Gibbium boieldieui, **287, 290.**
Gibbium psylloides, **287, 289, 290, 294, 295, 297, 301, 304, 308, 309, 313.**
gibboides, *Sphaericus.*
gibbosa, *Agathis.*
Gingelly Fly (see *Asphondylia sesami*).
globulus, *Paraniptus*; *Trigonogenius.*
Glossina, transect fly-rounds for studies of populations of, **275–285.**
Glossina austeni, population studies of, in Zanzibar, **277, 279, 280.**
Glossina fusca, in Nigeria, **597**; ecology of, **633–646**; trypanosomes in, **643, 644.**
Glossina haningtoni, **633** (note).
Glossina longipalpis, ecology of, in Nigeria, **595–615**; trypanosomes in, **612, 613.**
Glossina medicorum, in Nigeria, **597**; ecology of, **633, 634, 635, 642, 643**; trypanosomes in, **643.**
Glossina morsitans, **644.**
Glossina nashi, **633** (note).
Glossina nigrofusca, ecology of, in Nigeria, **633, 634, 636, 637, 642, 643**; trypanosomes in, **643, 644.**
Glossina pallicera, **633, 637.**
Glossina pallidipes, population studies of, in East Africa, **275, 277, 278, 279, 280.**

Glossina palpalis, in Ghana, **183–189**; in Nigeria, **449–465, 597, 617–631, 633**; *Trypanosoma* spp. in, **625, 626**; infectibility of, with *T. vivax*, **183–189**; ecology of, **617–631**; obstructive clearing against, **449–465**.
Glossina palpalis fuscipes, **277**.
Glossina swynnertoni, population studies of, in Tanganyika, **275, 276, 277, 278, 279, 280**.
Glossina tabaniformis, ecology of, in Nigeria, **633–646**; trypanosomes in, **643, 644**.
Glossina tachinoides, in Ghana, **183–189**; in Nigeria, **449, 451, 454, 459, 460, 462, 597**; infectibility of, with *Trypanosoma vivax*, **183–189**; effects of obstructive clearing on, **449, 451, 454, 459, 460, 462**.
Glycyphagus destructor, **303**.
Glycyphagus domesticus, **303**.
Gnorimoschema operculella, biological control of, in Bermuda, **426, 434**.
Goats, Anophelines feeding on, **654**; experiments with *Glossina* and *Trypanosoma vivax* in, **183–189**; not poisoned by feeding on dieldrin-sprayed vegetation, **384**.
godeffroyi, *Strumigenys*.
Gonocephalum, **261**.
gorhami, *Prodilis*.
gossypiella, *Platyedra*.
gossypii, *Phenococcus*.
Gossypium (see Cotton).
Gout Fly (see *Chlorops pumilionis*).
grahami, *Culex*; *Eretmapodites*.
granarium, *Trogoderma*.
granella, *Nemapogon*.
Grasses, insects infesting, in Britain, **39–52, 53–62**.
gregaria, *Schistocerca*.
Groundnuts, *Heliothis armigera* on, in Uganda, **488, 493, 499, 502**.
guerini, *Polyrhachis*.
Guiana, British, *Ancylostomia stercorea* in, **737**; parasite of *A. stercorea* in, **750**.
guiarti, *Culex*.
Guineacorn (see Sorghum).
guineense, *Tetramorium*.
gularis, *Aphomia*.
Guthion, against *Scotinophara lurida*, **717–735**.
Gynopterus (see *Ptinus*).

H.

Habrolepis rouxi, **427**.
haematodes, *Odontomachus*.
haningtoni, *Glossina*.
Harlequin Bug (see *Murgantia histrionica*).
hawaiiensis, *Coccophagus*.
haworthi, *Aëdes* (*Aëdimorphus*).
hebetor, *Bracon*.
Hecabolus sulcatus, **303**.
Hedomyrma (see *Polyrhachis*).
heischi, *Aëdes* (*Stegomyia*).
Helianthus annuus (see Sunflower).
Heliothis armigera, effects of DDT sprays on, on cotton in Sudan, **577, 580, 581**; bionomics and rearing of, on cotton, etc., in Uganda, **487–506**.
Helopeltis, bionomics and control of, on cashew in Tanganyika, **171–181**.
Helopeltis anacardii, **171, 172, 173**.
Helopeltis bergrothi, **171, 172**.
Helopeltis schoutedeni, **171**.
Hemiberlesia lataniae, **151**.
Hemicnetha (see *Simulium*).
Hemisarcoptes malus, **427, 428**.
hemisphaerica, *Saissetia* (see *S. coffeae*).
hesperidum, *Coccus*.
Hevea brasiliensis (see Rubber).
Hibiscus, Coccids on, **431**.
hilleri, *Pseudeurostus*.
hirta, *Mycetaea*.
histrionica, *Murgantia*.
Hodgesia cyptopus, **228**.
Hoffmannophila pseudospretella, **303**.
Hog, Red River (see *Potamochoerus porcus*).
Holcus lanatus, Dipterous larvae injuring, **54, 55, 56, 58, 61**.
Holland, strain of *Amphorophora rubi* on raspberry in, **86**.
hololeucus, *Niptus*.
Honduras, British, Simuliids of, **703–710**.
Horismenus, **754**.
Horismenus floridanus, **754**.
horridus, *Culex* (*Neoculex*).
Horse, Anophelines feeding on, **654**.
horticola, *Anomala* (*Phyllopertha*).
House-fly (see *Musca domestica*).
Howardia biclavis, **428**.
humilis, *Iridomyrmex*; *Opius*.
Hybolasioptera, **661**.
Hydrellia incana, injuring grasses in England, **54, 58**.
hylas, *Platytelenomus*.
Hyperaspis jucunda, **430**.
Hyperaspis lateralis, **430**.
Hypoaspis, **303**.
Hypotrigona, **160**.

I.

Icerya purchasi, biological control of, in Bermuda, **423, 424, 434**.

iceryae, Cryptochetum.
impunctatus, Culicoides.
incana, Hydrellia.
inconspicuosus, Culex (*Mochthogenes*).
India, pests of tea in, **265–274, 437–448;** ants associated with Coccids in, **437–448;** natural enemies of Coccids in, **439, 440, 443, 444.**
Indonesia, Xyloryctids on rubber and *Schleichera trijuga* in, **9, 10;** Anophelines and malaria in, **647–660.**
ingrami, Aëdes (*Finlaya*).
insidiosa, Pentilia.
insignis, Culex (*Neoculex*).
insulana, Earias.
insularis, Parachernes (*Argentochernes*).
interpunctella, Plodia.
invidiosus, Culex.
Iranolin 2241, **379.**
Iranolin KEB, **379.**
Ireneidris myops, **116, 118, 132, 550, 551, 552, 553, 555.**
Iridomyrmex anceps, **118.**
Iridomyrmex anceps papuana, **116, 132.**
Iridomyrmex humilis, **424, 430, 433.**
Iridomyrmex myrmecodiae, relation of, to *Amblypelta* and nutfall of coconuts in Solomon Is., **97–133, 523–558, 559, 565.**
irritans, Camponotus.
Isodrin, against *Scotinophara lurida*, **723, 724, 732.**
isolatus, Apanteles etiellae.

J.

jamaicensis, Exochomus.
japonicus, Ptinus (*Cyphoderes*).
Jauravia, **272.**
johnsoni, Ooencyrtus.
jucunda, Hyperaspis.
Juniperus (Juniper), Coccids infesting species of, in Bermuda, **423, 426, 427, 428, 429, 432.**
Jute, *Oligonychus coffeae* on, in India, **265–274.**

K.

kabwachensis, Aëdes (*Aëdimorphus*) *abnormalis.*
Kenya Colony, *Glossina pallidipes* in, **278–279;** mosquitos in, **191–208, 687–696, 759, 768, 775.**
Kerosene, in seed dressings against *Delia antiqua*, **799, 800, 801, 802, 803, 805.**
Khapra Beetle (see *Trogoderma granarium*).
Kobus defassa unctuosus, **609.**
kochi, Anopheles.
koehleri, Arrenoclavus.
kotinskyi, Microterys.
kühniella, Anagasta.

L.

Lachesilla pedicularia, **712.**
laeviscutellum, Tyndarichus.
Laingiococcus painei, **538.**
lamborni, Aëdes (*Aëdimorphus*).
Lamoria, **160.**
laphygmarum, Meteorus.
lardarius, Dermestes.
Lariophagus distinguendus, **303.**
Lasioptera, **661.**
lataniae, Hemiberlesia.
lateralis, Hyperaspis.
latro, auct., *Ptinus* (see *P. clavipes mobilis*).
latus, Poecilocoris.
lecanii, Coccophagus (see *C. lycimnia*).
Lepidosaphes newsteadi, biological control of, in Bermuda, **423, 426–429.**
Lepidosaphes ulmi, **427.**
Lepinotus patruelis, **712.**
Leptogenys diminuta santschi, **132.**
Leptohylemyia coarctata, **59, 61.**
leptolabis, Aëdes (*Aëdimorphus*).
Leptomastidea abnormis, **430.**
Leptomastix dactylopii, **430.**
Leucaspis loewi, **427, 428.**
leucotreta, Argyroploce.
leveri, Pseudococcus.
Libya, *Schistocerca gregaria* in, **381–382, 384.**
lichenum, Ptinus (*Pseudoptinus*).
Lindane (see BHC).
Lindorus lophanthae, **424, 425, 427, 428, 433.**
lineatopennis, Aëdes (*Banksinella*).
lingnanensis, Aphytis.
Linnaemyia agilis, **501.**
Linnaemyia longirostris, **501.**
Lioscymnus diversipes, **427.**
Litomastix, **667.**
Lizards (see *Anolis* and *Varanus*).
Lobopelta (see *Leptogenys*).
Locust, Desert (see *Schistocerca gregaria*).
Locust, Red (see *Nomadacris septemfasciata*).
loewi, Leucaspis.
Lolium spp., Dipterous larvae injuring, **54, 55, 56, 58, 59.**
longicornis, Paratrechina.
longinoda, Oecophylla.
longipalpis, Aëdes (*Finlaya*); *Glossina.*
longipes, Anoplolepis.

longirostris, *Linnaemyia*.
lophanthae, *Lindorus*.
Lotis neglecta, **427, 428.**
Lotis nigerrima, **427, 428.**
lounsburyi, *Aspidiotiphagus*.
Loxodonta africana, **609, 625.**
Lucilia sericata, **156.**
lurida, *Scotinophara*.
luteipes, *Azya*.
luteolus, *Aphycus* (*Metaphycus*).
lutescens, *Toxorhynchites*.
Lutzia (see *Culex*).
lybica, *Empoasca*.
lycimnia, *Coccophagus*.
Lyctocoris campestris, **712.**

M.

maculatus, *Anopheles*; *Callosobruchus*; *Camponotus*.
maculipalpis, *Anopheles*.
Maize, *Oscinella frit* on, in Britain, **61**; *Busseola fusca* on, in S. Rhodesia, **809–819**; *Heliothis armigera* on, in Uganda, **487–506.**
malaitensis, *Amblypelta cocophaga*.
Malaria, relation of Anophelines to, in Java, **647, 658, 659.**
Malathion, against Diptera, **72, 782, 783, 784**; against *Scotinophara lurida*, **717–735.**
Malaya, *Deloryctis corticivora* on rubber in, **9.**
malayensis, *Anopheles subpictus*.
Maltings, *Trogoderma granarium* in, in Britain, **407–422.**
malus, *Hemisarcoptes*.
mangiferae, *Coccus*.
Manihot esculenta (Cassava), ant associated with *Amblypelta* on, **114, 121.**
manni, *Opisthopsis*; *Paratrechina*.
Mansonia (*Taeniorhynchus*) *africana*, **193, 194, 196, 199, 200, 228, 688.**
Mansonia (*Taeniorhynchus*) *chrysosoma*, **196.**
Mansonia fuscopennata, **228.**
Mansonia (*Taeniorhynchus*) *uniformis*, **193, 196, 199, 200, 228, 688.**
Mansonioides (see *Mansonia*).
Maruca testualis, **737, 754.**
mauritanicus, *Tenebroides*.
Mauritius, parasites of *Ancylostomia stercorea* introduced into, against Pyralids on pigeon pea, **737, 754, 755.**
medicorum, *Glossina*.
mediopunctatus, *Aëdes* (*Aëdimorphus*) *cumminsi*.
megacephala, *Pheidole*.
Melanagromyza phaseoli, life-history and control of, on beans in Tanganyika, **781–793.**
melanocephalum, *Tapinoma*.
Meliola, **440.**
mellifera, *Apis*.
Melon, injured by 10 DRDK, **157.**
membranaceus, *Brachytrupes*.
Meranoplus, **438.**
mercator, *Oryzaephilus*.
meridionalis, *Elachertus*.
Meromyza, injuring grasses in England, **54, 58, 61.**
Meromyza saltatrix, **55.**
Meromyza variegata, **55.**
metallicum, *Simulium*.
metallicus, *Aëdes* (*Stegomyia*).
Metaphycus (see *Aphycus*).
Metarrhizium anisopliae, **91, 92, 93.**
Metasystox, against *Scotinophara lurida*, **727, 728, 729, 730, 731, 733.**
Meteorus laphygmarum, **501.**
mexicanum, *Simulium* (*Hemicnetha*).
mexicanus, *Coccophagus*.
Mezium, **287.**
Mezium affine, **287–326.**
Mezium americanum, **287, 289, 290, 296, 297.**
Mezium natalense, **287, 290.**
Mezium sulcatum, **287.**
Microdon, **444.**
Microdon bellus, **440, 444.**
Microterys kotinskyi, **431.**
Microweisia misella, **427.**
Microweisia suturalis, **427, 428.**
Middleburg Virus, **775.**
Mimomyia (see *Ficalbia*).
mimomyiaformis, *Ficalbia* (*Mimomyia*).
mimula, *Conioscinella*.
minima, *Carulaspis*.
minutula, *Paratrechina*.
minutus, *Enicmus*.
misella, *Microweisia*.
mobilis, *Ptinus clavipes*.
Mochthogenes (see *Culex*).
modiglianii, *Technomyrmex*.
moluccana, *Acropyga*.
Monkey, Mona (see *Cercopithecus mona*).
Monkey, Patas (see *Erythrocebus patas*).
Monkey, Tantalus Guenon (see *Cercopithecus aethiops tantalus*).
Monomorium, **116, 132.**
Monomorium floricola, **107, 116, 118, 132.**
Monomorium fraterculus, **116.**
Monomorium pharaonis, **116.**
montrouzieri, *Cryptolaemus*.
Montserrat, *Ancylostomia stercorea* in, **737.**

Moonlight, effect of, on emergence of Chironomids, **1–8.**
morsitans, *Glossina.*
moucheti, *Culex.*
Mucidus (see *Aëdes*).
mucidus, *Aëdes.*
Murgantia histrionica, biological control of, in Bermuda, **429.**
Musca domestica, deposition of airborne droplets on dead, **327–332.**
mutilis, *Aëdes* (*Aëdimorphus*).
Mycetaea hirta, **712.**
Myiophagus ucrainica, **428.**
myops, *Ireneidris.*
Myopsocnema annulata, **712.**
Myrma (see *Polyrhachis*).
Myrmatopa (see *Polyrhachis*).
myrmecodiae, *Iridomyrmex.*
myrmecophila, *Cordyceps.*
Myrmegonia (see *Camponotus*).
mytilaspidis, *Aphytis.*
Myzomyia (see *Anopheles*).
Myzus persicae, used in tests of systemic action of insecticides, **25–38.**

N.

Nacoleia octasema (Banana Scab Moth), new parasite and hyperparasite of, in New Guinea, **667–670.**
nacoleiae, *Pseudolitomastix.*
nashi, *Glossina.*
natalense, *Mezium.*
natronius, *Aëdes* (*Aëdimorphus*).
Nausibius clavicornis, biology of, on sugar in Trinidad, **237–258.**
Neanastatus africanus, **666.**
neavei, *Simulium.*
nebulosus, *Culex* (*Culiciomyia*).
neglecta, *Cetema*; *Lotis.*
Nemapogon granella, **712, 713, 714.**
Neochelonella curvimaculata, **501.**
Neoculex (see *Culex*).
Nerium oleander (see Oleander).
Netelia capensis, **501.**
New Guinea, new parasite and hyperparasite of *Nacoleia octasema* in, **667–670.**
newsteadi, *Lepidosaphes.*
niger, *Thysanus.*
Nigeria, Cecidomyiids on cereals in, **661–666**; *Callosobruchus maculatus* on cowpea in, **671–680**; *Aëdes aegypti* in, **681–686**; *Glossina* spp. and trypanosomes in, **449–465, 595–615, 617–631, 633–646.**
nigerrima, *Lotis.*
nigra, *Saissetia*; *Stomoxys.*
nigritus, *Chilocorus.*
nigrofusca, *Glossina.*
nindi, *Pheidole.*
nipae, *Nipaecoccus.*
Nipaecoccus nipae, biological control of, in Bermuda, **425.**
Nipaecoccus vastator, **438, 439.**
Niptus, **288.**
Niptus hololeucus, **287–326.**
Niptus ventriculus, **289, 297.**
nitida, *Tetsimia.*
nitidissima, *Oscinella.*
njalensis, *Pseudococcus.*
nodiceps, *Cryptognatha.*
Nomadacris septemfasciata, effects of vegetation, climate and weather on, in Tanganyika, **333–353, 507–521.**
novemnotata, *Coccinella.*
Novosol, **379.**
Ntaya Virus, **773.**
nuda, *Cardiocondyla.*

O.

Oak, Ceylon (see *Schleichera trijuga*).
Oats, *Oscinella frit* on, **55, 59, 61.**
oblonga, *Vollenhovia.*
obnigra, *Crematogaster* (*Acrocoelia*).
obsoletus, *Carpophilus.*
Obstructive Clearing, against *Glossina*, **449–465.**
occidentalis, *Cephaloscymnus.*
oceanica, *Pheidole.*
oceanicus, *Anochetus punctiventris.*
Ochlerotatus (see *Aëdes*).
ochraceum, *Simulium.*
ochraceus, *Aëdes* (*Aëdimorphus*).
octasema, *Nacoleia.*
Odontomachus haematodes, **116, 117, 118, 132, 542, 552.**
Odontomachus saevissimus, **132, 552.**
odoratum, *Anthoxanthum.*
Oecophylla longinoda, relation of, to *Pseudotheraptus wayi* on coconut in Zanzibar, **135–149, 151**; effects of insecticides on, **151–164.**
Oecophylla smaragdina, relation of, to Coccids on tea in India, **437–448**; relation of, to *Amblypelta* and nutfall of coconuts in Solomon Is., **97–133, 523–558, 565.**
Oils, in seed dressings against *Delia antiqua*, **799, 800, 801, 802, 803, 805.**
oleae, *Saissetia.*
Oleander, Coccids on, **424, 430, 431.**
Oligomyrmex viehmeyeri, **116.**
Oligonychus coffeae, bionomics of, on tea in India, **265–274.**
Oligonychus ununguis, biological control of, in Bermuda, **432,**
Onchocerciasis, **703, 704.**

Onion, seed treatments of, against *Delia antiqua* in Britain, **795–807.**
Onion Thrips (see *Thrips tabaci*).
Ooencyrtus, **429.**
Ooencyrtus johnsoni, **429.**
operculella, Gnorimoschema.
Opisthopsis manni, **133.**
Opius humilis, **424.**
Opomyza, **61.**
Opomyza florum, **60.**
Opomyza germinationis, on wheat and grasses in England, **54, 56, 58, 59.**
Opomyza petrei, on grasses in England, **54, 56, 58, 61.**
Orcus chalybeus, **427.**
ornata, Zagloba.
ornatothoracis, Culex.
Orthocrema (see *Crematogaster*).
Oryctes, **160.**
Oryza sativa (see Rice).
oryzae, Calandra; *Pachydiplosis.*
Oryzaephilus mercator, **252, 256.**
Oryzaephilus surinamensis, **712, 713, 714, 715.**
osae, Polyrhachis (*Myrmatopa*).
Oscinella, study on species of, infesting cereals and grasses in England, **53–62.**
Otala lactea, **432.**

P.

Pachydiplosis oryzae, on rice in Nigeria, **664, 665.**
painei, Laingiococcus.
palliatus, Ptinus (*Gynopterus*).
pallicera, Glossina.
pallidipes, Glossina.
pallidus, Acerophagus.
Palloptera quinquemaculata, injuring grasses in England, **54, 58.**
Palmetto Scale (see *Comstockiella sabalis*).
palpalis, Aëdes (*Banksinella*); *Glossina.*
Paltothyreus tarsatus, **91.**
paludis, Anopheles.
Paniscus, auct. (see *Netelia*).
papuana, Acropyga moluccana; *Iridomyrmex anceps.*
Parachernes insularis, **565.**
Paraniptus, **288.**
Paraniptus globulus, **289, 291.**
parasitica, Sturmiopsis.
Paratemnus ellingseni, **565.**
Paratemnus salomonis, **565.**
Parathion, against *Melanagromyza phaseoli*, **784, 785**; against *Scotinophara lurida*, **717–735.**
Paratrechina, **118, 133, 438, 542.**
Paratrechina bourbonica, **133.**
Paratrechina longicornis, **133, 152, 156.**
Paratrechina manni, **116, 117, 118, 133, 551, 552, 554.**
Paratrechina minutula, **551, 552, 553.**
Paratrechina minutula atoma, **116, 117, 133, 550, 551, 553, 555.**
Paratrechina stigmatica, **133.**
Paratrechina vaga, **116, 117, 133.**
Paratrechina vividula, **116, 117, 133, 527, 550, 551, 552, 553, 554, 555.**
patruelis, Lepinotus.
Pauridia peregrina, **430.**
pedestris, Vollenhovia oblonga.
pedicularia, Lachesilla.
Pediculoides ventricosus, **303.**
pembaensis, Aëdes (*Skusea*).
pennipes, Trichopoda.
pentagona, Pseudaulacaspis.
Pentilia, **427.**
Pentilia castanea, **427.**
Pentilia confluens, **427.**
Pentilia insidiosa, **425, 427, 428.**
perdignus, Pseudaphycus.
peregrina, Pauridia.
peregrinus, Tetracnemus.
perfuscus, Culex.
Perilampus, **754.**
Perilampus tristis, **501.**
Perisierola, bionomics and rearing of, parasitising *Ancylostomia stercorea* in Trinidad, **738, 750–753**; introduced into Mauritius, **755.**
perniciosi, Prospaltella.
persicae, Myzus.
petrei, Opomyza.
Phaeosaccardinula theae, **440.**
Phalaris tuberosa, Dipterous larvae injuring, **58.**
Phanerotoma bennetti, **746, 754**; bionomics and rearing of, parasitising *Ancylostomia stercorea* in Trinidad, **738, 741–744**; introduced into Mauritius, **755.**
pharaonis, Monomorium.
pharoensis, Anopheles (*Myzomyia*).
Pharoscymnus exiguus, **427, 428.**
phaseoli, Melanagromyza.
Phaseolus vulgaris (see Beans).
Pheidolacanthinus, **107, 132.**
Pheidolacanthinus belli, **116.**
Pheidolacanthinus fuscescens, **116.**
Pheidolacanthinus sexspinosus, **116, 117, 118, 132, 550, 552, 553, 554.**
Pheidole, effects of insecticides on, **132, 136, 137, 139, 142, 152, 154, 156, 160.**
Pheidole megacephala, **433**; relation of, to *Amblypelta* and nutfall of coconuts in Solomon Is., **97–133, 523–558.**
Pheidole nindi, **132, 555.**
Pheidole oceanica, **116, 117, 132, 550, 551, 552, 553, 554.**

Pheidole philemon, **132.**
Pheidole punctulata, relation of, to *Pseudotheraptus wayi* on coconut in Zanzibar, **135–149.**
Pheidole sulcaticeps punensis, **438.**
Pheidole umbonata, **116, 117, 132, 552, 554, 555.**
Phenacoccus gossypii, biological control of, in Bermuda, **429, 430.**
philemon, *Pheidole*.
Phleum pratense, Dipterous larvae injuring, **58.**
Phorbia genitalis, **61.**
phthorimaeae, *Campoplex*; *Chelonus*.
phyllolabis, *Aëdes* (*Aëdimorphus*).
Phyllopertha (see *Anomala*).
Physcus, **425.**
picipes, *Stethorus*.
picta, *Cleis*.
picticornis, *Spiloconis*.
Pieris brassicae, used in tests of systemic action of insecticides, **25–38.**
Pig, *Glossina* spp. feeding on, **637.**
Pigeon Pea (see *Cajanus cajan*).
pipiens, *Culex*.
Pitangus sulphuratus, possible use of, in connection with biological control of Coccids in Bermuda, **432.**
Pittosporum, Coccids on, **430.**
Plagiolepis foreli, **133.**
Planococcus citri, **209, 542**; biological control of, in Bermuda, **429, 430.**
platycephalus, *Egius*.
Platyedra gossypiella, **577, 580.**
Platytelenomus hylas, **501.**
Plectropterus gambensis, **183, 184, 185.**
Plodia interpunctella, **712, 713, 714, 744.**
plumosa, *Ficalbia* (*Mimomyia*).
Poa spp., Dipterous larvae injuring, **56, 58.**
Poecilocoris latus, **442.**
poicilipes, *Culex*.
Polyrhachis, **152.**
Polyrhachis affinis, **438, 439.**
Polyrhachis annae, **133, 552.**
Polyrhachis guerini, **116.**
Polyrhachis osae, **133, 552.**
Polyrhachis rastellata fulakora, **133.**
Polyrhachis rere, **133.**
Polyrhachis salomo, **116, 117, 118, 133, 550, 552.**
Ponera, **132.**
Ponera pruinosa, **116.**
Pongola Virus, **774.**
Porcupine (see *Atherurus africanus*).
Poria, **427.**
portoricensis, *Encarsia*.
Potamochoerus porcus, **609, 625, 637, 643.**
Povilla adusta, **6.**
Pristhesancus browni, **565.**
Pristomerus fumipennis, **501.**
Pristomyrmex, **132.**
Prochiloneurus, **431.**
proclia, *Aphytis*.
Procula douei, **427.**
Prodilis, **427.**
Prodilis gorhami, **425.**
profuga, *Schizonycha*.
Prolasioptera, **661.**
Prospaltella, **428.**
Prospaltella aurantii, **427.**
Prospaltella berlesei, **424.**
Prospaltella diaspidicola, **424.**
Prospaltella perniciosi, **424.**
pruinosa, *Ponera*.
Psammodes scrobicollis, in tobacco fields in S. Rhodesia, **90, 259–263.**
Psammodes similis, in tobacco fields in S. Rhodesia, **90, 259–263.**
Pseudaphycus angelicus, **430.**
Pseudaphycus perdignus, **430.**
Pseudaphycus utilis, **425.**
Pseudaulacaspis pentagona, biological control of, in Bermuda, **424, 425, 428, 434.**
Pseudeurostus, **288.**
Pseudeurostus hilleri, **287–326.**
Pseudobruchus (see *Ptinus*).
pseudococci, *Anagrus*.
Pseudococcus, **177, 429.**
Pseudococcus adonidum, **542**; biological control of, in Bermuda, **429, 430.**
Pseudococcus leveri, **542.**
Pseudococcus njalensis, **209.**
Pseudolitomastix nacoleiae, gen. et sp. n., parasite of *Nacoleia octasema* in New Guinea, **667**; parasite of, **670.**
Pseudoptinus (see *Ptinus*).
pseudospretella, *Hoffmannophila*.
Pseudotheraptus wayi (on coconut in Zanzibar), damage caused by, **135–149**; relation of ants to, **135–149, 151–164**; insecticides against, **151–164.**
psidii, *Pulvinaria*.
Psilopelmia (see *Simulium*).
psylloides, *Gibbium*.
Ptinids, studies on, **287–326.**
ptinivorus, *Cryptus*.
Ptinus agnatus, **288, 297.**
Ptinus bicinctus, **288, 291, 297.**
Ptinus californicus, **288, 289, 292, 298, 299, 304, 307, 313, 314.**
Ptinus clavipes, **287–326.**
Ptinus clavipes mobilis (*P. latro*, auct.), **287–326.**
Ptinus coarcticollis, **288, 298.**
Ptinus exulans, **288, 292, 296, 298, 299, 300, 313.**

Ptinus fur, **287–326, 712.**
Ptinus gandolphei, **288, 292, 298.**
Ptinus japonicus, **288, 293.**
Ptinus latro, auct. (see *P. clavipes mobilis*).
Ptinus lichenum, **288, 295, 296, 300, 301.**
Ptinus palliatus, **288, 295, 296, 300, 301.**
Ptinus pusillus, **287–326.**
Ptinus raptor, **288, 289, 293, 296, 298, 299, 300, 308.**
Ptinus rufipes, **288, 293, 295, 298.**
Ptinus sexpunctatus, **287–326.**
Ptinus subpilosus, **288, 295, 296, 298, 299, 301.**
Ptinus tectus, **287–326.**
Ptinus vaulogeri, **288, 298, 299, 313.**
Ptinus villiger, **287–326.**
Ptochoryctis chalazopa, on rubber in Java, **10.**
pulverulentum, *Simulium* (*Hemicnetha*).
Pulvinaria psidii, biological control of, in Bermuda, **428, 431, 432, 434.**
pulvinariae, *Cheiloneurus*.
pumilionis, *Chlorops*.
punctiventris, *Anochetus*.
punctocostalis, *Aëdes* (*Banksinella*).
punctulata, *Pheidole*.
punensis, *Pheidole sulcaticeps*.
purchasi, *Icerya*.
pusillus, *Bothriomyrmex*; *Ptinus*.
Pyrethrins, **161.**

Q.

quadridentata, *Euponera stigma*.
quadripustulatus, *Exochomus*.
quadrivittatum, *Simulium* (*Byssodon*).
queenslandensis, *Aëdes aegypti*.
quinquemaculata, *Palloptera*.
quinquevittatus, *Eretmapodites*.

R.

raptor, *Ptinus* (*Cyphoderes*).
Raspberry, strains of *Amphorophora rubi* on, in England and Holland, **81–87.**
rastellata, *Polyrhachis* (*Cyrtomyrma*).
rennellensis, *Amblypelta costalis*.
rere, *Polyrhachis* (*Charyomyrma*).
reticulatus, *Camponotus*.
revestita, *Zenoria*.
revoluta, *Cycas*.
Rhachiocrema (see *Crematogaster*).
Rhodesia, Northern, *Chironomus brevibucca* in, **1–8.**
Rhodesia, Southern, *Busseola fusca* on maize in, **809–819;** pests of tobacco in, **89–96, 259–263;** fungous diseases of Lamellicorn larvae in, **89–96.**
rhodesiensis, *Anopheles* (*Myzomyia*).
Rhytidoponera froggatti, **132.**
Rice, *Scotinophara lurida* on, in Ceylon, **717–735;** *Pachydiplosis oryzae* on, in Nigeria, **664, 665.**
Rice, Stored, *Calandra oryzae* on, **697–702.**
Rice Stem Gall Midge (see *Pachydiplosis oryzae*).
Rift Valley Fever Virus, **773, 774.**
ritchiei, *Exochomus*.
Rodolia cardinalis, **423, 434.**
Rogeria, **132.**
Rotenone, **161.**
rouxi, *Habrolepis*.
Rubber, Xyloryctids on, in Malaya and Indonesia, **9, 10.**
rubi, *Amphorophora*.
Rubus spp., experiments with strains of *Amphorophora rubi* and, **81–87.**
rudnevi, *Tyndarichus*.
rufifrons, *Cybocephalus*.
rufilatus, *Cephalophus*.
rufipes, *Ptinus* (*Bruchoptinus*).
rufithorax, *Anastatus axiagasti*.
rufoglaucus, *Camponotus*.
Rumina decollata, **432.**
Rye, *Oscinella frit* on, **61.**

S.

Sabal bermudiana, *Comstockiella sabalis* on, **425.**
sabalis, *Comstockiella*.
sabulosum, *Stiphrosoma*.
saevissimus, *Odontomachus*.
Sago Palm (see *Cycas revoluta*).
Sahlbergella singularis, insecticides against, on cacao in Ghana, **13–23;** method of rearing, **11–12.**
Saissetia coffeae, biological control of, in Bermuda, **428, 431;** ant associated with, on tea in India, **438.**
Saissetia formicarii, relation of ants to, on tea in India, **437–448.**
Saissetia hemisphaerica (see *S. coffeae*).
Saissetia nigra, biological control of, in Bermuda, **428, 431;** ants associated with, on tea, etc., in India and Solomon Is., **538, 542.**
Saissetia oleae, **542;** biological control of, in Bermuda, **431.**
salomo, *Polyrhachis* (*Myrma*).
salomonis, *Paratemnus*.
saltatrix, *Meromyza*.
samboni, *Simulium* (*Psilopelmia*).
samoaensis, *Camponotus irritans*.
sanctae crucis, *Camponotus*.

sanguinea, *Cycloneda*.
santschi, *Leptogenys* (*Lobopelta*) *diminuta*.
sasakii, *Calandra*.
scatophagoides, *Aëdes* (*Mucidus*).
scaurus, *Tyndarichus*.
Schistocerca gregaria, in Eritrea, **378, 379, 380, 381**; in Ethiopia, **374, 382, 383**; in Libya, **381, 382, 384**; methods of spraying vegetation against, **355–370, 371–386**.
Schizonycha profuga, in tobacco fields in S. Rhodesia, **89–96, 259–263**; fungous diseases of, **89–96**.
Schleichera trijuga, *Deloryctis corticivora* on, in Malaya, **9**.
schoutedeni, *Helopeltis*.
Schradan, tests of systemic and insecticidal action of, **25–38**.
scita, *Crematogaster* (*Acrocoelia*).
Scotinophara lurida, insecticides against, on rice in Ceylon, **717–735**.
scrobicollis, *Psammodes*.
Scymnus, **272, 427**.
Scymnus binaevatus, **425**.
Scymnus coccivora, **432**.
Scymnus sordidus, **430**.
Seius, **303**.
semibrunneus, *Culex* (*Culiciomyia*).
Semidalis aleyrodiformis, **427**.
Semliki Forest Virus, **772, 774**.
semlikiensis, *Aëdes* (*Aëdimorphus*).
septemfasciata, *Nomadacris*.
Septobasidium bogoriense, **440**.
Septobasidium pilosum, **440**.
Septobasidium theae, **440**.
Septobasidium tuberculatum, **440**.
sericata, *Lucilia*.
sesami, *Asphondylia*.
Sesamum orientale, *Asphondylia sesami* on, in Nigeria, **665**.
sexpunctatus, *Ptinus* (*Gynopterus*).
sexspinosus, *Pheidolacanthinus*.
Sheep, not poisoned by feeding on dieldrin-sprayed vegetation, **384**.
Sida rhombifolia, *Saissetia* spp. on, **542**.
Sierra Leone, *Calandra oryzae* on stored rice in, **697**.
silvestris, *Eretmapodites*.
Simbu Virus, **775**.
similis, *Psammodes*.
simillimum, *Tetramorium*.
simillina, *Cryptognatha*.
simpsoni, *Aëdes* (*Stegomyia*); *Culex*.
Simsin (see *Sesamum orientale*).
simulans, *Aëdes* (*Aëdimorphus*).
Simuliids, of British Honduras, **703–710**.
Simulium callidum, **706, 707**.
Simulium damnosum, **707**.
Simulium dugesi, **706**.
Simulium earlei, **706, 707**.
Simulium metallicum, **706, 707, 708, 709**.
Simulium mexicanum, **706, 707**.
Simulium neavei, **708**.
Simulium ochraceum, **706**.
Simulium pulverentulum, **706, 707, 708**.
Simulium quadrivittatum, **705, 706, 707, 708, 709**.
Simulium samboni, **706, 707, 708**.
Simulium veracruzanum, **706, 707, 708**.
Simulium virgatum, **706, 707**.
singularis, *Sahlbergella*.
sitiens, *Culex*.
Skusea (see *Aëdes*).
Sleeping Sickness, **626**. (See *Trypanosoma gambiense*).
smaragdina, *Oecophylla*.
smithburni, *Aëdes* (*Aëdimorphus*).
Sodium Fluoroacetate, tests of systemic and insecticidal action of, **25–38**.
Solomon Islands, *Amblypelta* and associated ants in relation to nutfall of coconuts in, **97–133, 523–558, 559–566**.
sordidus, *Scymnus*.
sorghivora, *Thomasiella*.
Sorghum vulgare (see Sorghum).
Sorghum, new Cecidomyiid on, in Nigeria, **661, 663, 664**; *Heliothis armigera* reared on, **496**.
Sorghum Stem Gall Midge (see *Thomasiella sorghivora*).
Spalgis epius, **439, 443, 444**.
Spathius exarator, **303**.
Sphaericus brasiliensis, **289, 290**.
Sphaericus gibboides, **289, 290**.
Spiloconis picticornis, **425**.
splendens, *Ficalbia* (*Mimomyia*).
Sprays, methods of applying, to vegetation against locusts, **355–370, 371–386**.
Spurwing Goose (see *Plectropterus gambensis*).
squamosum, *Stethomezium*.
squamosus, *Anopheles* (*Myzomyia*).
stanleyi, *Aphycus* (*Metaphycus*).
Stegomyia (see *Aëdes*).
stercorea, *Ancylostomia*.
Stethomezium, **287**.
Stethomezium squamosum, **287–326**.
Stethorus, **272**.
Stethorus picipes, **432**.
stigma, *Chilocorus*; *Euponera* (*Trachymesopus*).
stigmatica, *Paratrechina*.
Stiphrosoma sabulosum, injuring grasses in England, **54, 56, 58**.
stokesi, *Aëdes* (*Aëdimorphus*).
Stomoxys, attacking cattle in Uganda, **165**.

Stomoxys calcitrans, **156**; method of rearing, **165–169.**
Stomoxys nigra, **165.**
Strumigenys, **132.**
Strumigenys godeffroyi, **132, 552.**
Sturmiopsis parasitica, parasite of *Busseola fusca* in S. Rhodesia, **816.**
subfumatus, *Cryptophagus.*
subpictus, *Anopheles.*
subpilosus, *Ptinus.*
subsimplicipes, *Eretmapodites.*
Sudan, pests of cotton in, **567–594.**
Sugar, *Nausibius clavicornis* infesting, in Trinidad, **237–258.**
sulcaticeps, *Pheidole.*
sulcatum, *Mezium.*
sulcatus, *Hecabolus.*
Sunflower, *Heliothis armigera* on, in Uganda, **490, 491, 492, 498, 499, 502.**
surinamensis, *Oryzaephilus.*
suturalis, *Microweisia.*
swynnertoni, *Glossina.*
sydneyensis, *Anarhopus.*
Sylvicapra grimmia, **609, 625.**
Sympherobius barberi, **430.**
Syncerus nanus, **609.**

T.

tabaci, *Bemisia.*
tabaniformis, *Glossina.*
tachinoides, *Glossina.*
taeniarostris, *Aëdes* (*Banksinella*).
Taeniorhynchus (see *Mansonia*).
Tanganyika Territory, *Melanagromyza phaseoli* on beans in, **781–793**; *Glossina* spp. in, **275–285**; *Helopeltis* on cashew in, **171–181**; *Nomadacris septemfasciata* in, **333–353, 507–521.**
Tapinoma, **133.**
Tapinoma melanocephalum, **116, 118, 133, 550, 552, 553, 555, 565.**
Tapinoma timidum, **133.**
Tarichium uvella, **93.**
tarsalis, *Aëdes* (*Aëdimorphus*).
tarsatus, *Paltothyreus.*
taylori, *Aëdes.*
Tea, pests of, in India, **265–274, 437–448.**
Technomyrmex, **110.**
Technomyrmex albipes, **133.**
Technomyrmex detorquens, **116, 117, 118, 133, 438, 439, 530, 541, 550, 551, 552, 553, 554, 555.**
Technomyrmex detorquens vitiensis, **133.**
Technomyrmex modiglianii elatior, **438, 439.**
tectus, *Ptinus* (*Pseudobruchus*).
Teepol, **27, 30, 33, 34.**
Telsimia nitida, **427, 428.**
Temperature, effect of acclimatization on survival of *Aëdes aegypti* exposed to high and low, **821–823**; effects of, on growth and reproduction of *Dysdercus fasciatus*, **387–405.**
Tenebroides mauritanicus, **712.**
tenebrosus, *Anopheles coustani.*
tenuiclavus, *Tyrophagus.*
tessellatus, *Anopheles.*
testulalis, *Maruca.*
Tetracnemus peregrinus, **430.**
Tetramorium guineense, **132.**
Tetramorium simillimum, **132.**
Tetramorium tonganum, **132.**
Tetrastichus, **754.**
theae, *Eriochiton.*
theobroma, *Distantiella.*
Theridion familiare, **303.**
Thiram, **799, 801, 802, 806.**
Thomasiella, **661.**
Thomasiella sorghivora, sp. n., **661–664.**
thurberiphagae, *Bracon.*
Thyreophagus entomophagus, **303.**
Thysanus niger, **430.**
tigripes, *Culex* (*Lutzia*).
timidum, *Tapinoma.*
tineivorus, *Blattisocius.*
Tiphia, **262.**
Tipnus, **288.**
Tipnus unicolor, **287–326.**
Tobacco, pests of, in S. Rhodesia, **89, 259–263.**
tonganum, *Tetramorium.*
Torrubiella, **90, 91, 92.**
Toxaphene, against *Scotinophara lurida*, **722, 723, 732.**
Toxoptera aurantii, **444.**
Toxorhynchites brevipalpis, **193, 199.**
Toxorhynchites lutescens, **193.**
Trachymesopus (see *Euponera*).
Tragelaphus scriptus, **609, 625.**
Tribolium castaneum, **15, 16, 21, 712.**
Trichogramma, **429, 501.**
tricholabis, *Aëdes* (*Aëdimorphus*).
Trichopoda pennipes, **530, 565.**
trifoliatus, *Culex.*
Trigona, **160.**
Trigonogenius globulus, **287–326.**
trimaculatus, *Cardiochiles.*
Trinidad, *Ancylostomia stercorea* on pigeon pea in, **737–757**; parasites of *A. stercorea* introduced into Mauritius from, **737, 754, 755**; *Nausibius clavicornis* infesting sugar in, **237–258.**
trinitatis, *Azya.*
tripunctata, *Geomyza.*
tristis, *Perilampus.*
tritaeniorhynchus, *Culex.*

Trogoderma granarium, in stored products in Britain, **407–422, 712**; study on diapause larvae of, **407–422.**
tumidiventris, *Cryptognatha.*
Trypanosoma brucei, **612, 643, 644.**
Trypanosoma congolense, **612, 613, 625, 643, 644.**
Trypanosoma gambiense, **449, 626.**
Trypanosoma vivax, in *Glossina* spp., **612, 613, 625, 643, 644**; infectibility of *Glossina* spp. with, **183–189.**
Trypanosomiasis, of cattle, **165.** (See *Trypanosoma* spp.)
Tsetse Flies (see *Glossina*).
Tyndarichus clavatus, sp. n., **669.**
Tyndarichus laeviscutellum, **670.**
Tyndarichus rudnevi, **670.**
Tyndarichus scaurus, **669, 670.**
Tyrophagus tenuiclavus, **712.**

U.

Uganda, Lepidoptera on field crops in, **487–506**; *Aëdes* spp. and mosquito-borne diseases in, **227–235, 759–779**; *Stomoxys* attacking cattle in, **165**; parasites of *Heliothis armigera* in, **501, 502, 503, 504.**
Uganda S Virus, **774.**
ulmi, *Lepidosaphes.*
ultor, *Apanteles.*
umbonata, *Pheidole.*
unicolor, *Tipnus.*
uniformis, *Mansonia* (*Mansonioides*, *Taeniorhynchus*).
univittatus, *Culex.*
ununguis, *Oligonychus.*
Uranotaenia alboabdominalis, **193, 196.**
utilis, *Pseudaphycus.*

V.

vaga, *Paratrechina.*
vagus, *Anopheles.*
Varanus, **625, 732.**
variegata, *Meromyza.*
vastator, *Nipaecoccus*; *Oscinella.*
vaulogeri, *Ptinus* (*Gynopterus*).
ventricosus, *Pediculoides.*
ventriculus, *Niptus.*
veracruzanum, *Simulium* (*Psilopelmia*).
Verania vincta, **272.**
vexans, *Aëdes* (*Aëdimorphus*).
Vicia faba (see Beans, Broad).
viehmeyeri, *Oligomyrmex.*
Vigna unguiculata (see Cowpea).
villiger, *Ptinus.*
vincta, *Verania.*
virgata, *Ferrisiana.*
virgatum, *Simulium* (*Hemicnetha*).
viridis, *Coccus.*
vitiensis, *Technomyrmex detorquens.*
vittatus, *Aëdes* (*Stegomyia*).
vivax, *Trypanosoma.*
vividula, *Paratrechina.*
vividus, *Camponotus.*
Vollenhovia oblonga pedestris, **132.**
V.P. 2823, against *Melanagromyza phaseoli*, **786, 788, 789, 790.**

W.

Walnuts, Stored, pests in, **711–716.**
Waterbuck (see *Kobus defassa unctuosus*).
wayi, *Pseudotheraptus.*
Wedelia biflora, Coccids on, **542.**
weschei, *Culex.*
Wesselsbron Virus, **775.**
Wheat, pests of, in Britain, **59, 60, 61.**
wigglesworthi, *Aëdes* (*Aëdimorphus*); *Culex* (*Neoculex*).
" Williams' Mean ", **779.**

Y.

Yellow Fever, **772, 773.**

Z.

Zagloba ornata, **427, 428.**
Zanzibar, *Helopeltis* on cashew in, **171–181**; *Pseudotheraptus wayi* and associated ants on coconut in, **135–149, 151–164**; *Glossina austeni* in, **277, 279, 280.**
Zea mays (see Maize).
Zenoria revestita, **427.**
zetterstedtii, *Anabrolepis.*
ziemanni, *Anopheles coustani.*
zinckenella, *Etiella.*
Zophosis, **261.**

INDEX TO AUTHORS.

Bennett, F. D., **423, 737.**
Bradley, J. D., **9.**
Breese, M. H., **237.**
Briggs, J. B., **81.**
Brown, E. S., **97, 523, 559.**
Bünzli, G. H., **89, 259.**
Burges, H. D., **407.**
Büttiker, W. W., **89, 259.**

Carden, P. W., **795.**
Carnegie, A. J. M., **333.**
Caswell, G. H., **671.**
Chow, C. Y., **647.**
Clarke, K. U., **387.**
Coaker, T. H., **487.**
Courshee, R. J., **355.**

Das, G. M., **265, 437.**
David, W. A. L., **25.**
Davies, J. B., **449.**

Eady, R. D., **667.**

Fernando, H. E., **717.**
Ford, J., **275.**
Fryer, G., **1.**

Gardiner, B. O. C., **25.**
Garnham, P. C. C., **703.**
Glasgow, J. P., **275.**

Haddow, A. J., **759.**
Hanna, A. D., **209.**
Harris, K. M., **661.**
Heatherington, W., **209.**
Howe, R. W., **287.**
Hughes, I. W., **423.**

Ibnoe, R. M., **647.**

Jarman, R. T., **327.**
Johns, D. L., **275.**

Josopoero, S. T., **647.**
Joyce, R. J. V., **567.**

Kernaghan, R. J., **449.**
Kettle, D. S., **63.**

Lewis, D. J., **703.**

McClelland, G. A. H., **227, 687.**
Mapother, H. R., **209.**
Mellanby, K., **821.**
Milne, A., **39, 467.**

Nye, I. W. B., **53.**

Page, W. A., **595, 617, 667.**
Parish, J., **63.**
Parish, R. H., **63.**
Parr, H. C. M., **165.**
Prevett, P. F., **697.**

Raw, F., **11, 13.**

Sardesai, J. B., **387.**
Sayer, H. J., **371.**
Smith, K. G., **711.**
Smithers, C. N., **809.**
Squire, F. A., **183.**
Surtees, G., **681.**
Swaine, G., **171.**
Symmons, P., **333, 507.**

Teesdale, C., **191.**

Vanderplank, F. L., **135, 151.**

Walker, P. T., **781.**
Welch, J. R., **275.**
Wickens, R., **209.**
Wise, T. E., **237.**